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The importance of Southern Ocean frontal systems for the improvement of body condition in southern elephant seals

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Abstract

1. As top predators, it has been suggested that southern elephant seals serve as sentinels of ecosystem status to inform management and conservation.

2. This is because southern elephant seals annually undertake two large-scale foraging migrations for 2-3 and 7-8 months to replenish resources after fasting during breeding and moulting and often rely on dynamic macroscale latitudinal fronts to provide favourable foraging through aggregating prey.

3. Yet, it is largely unknown whether southern elephant seals respond to changes in frontal systems over the years, whether their foraging success is associated with specific frontal systems shifts, and how flexible southern elephant seals populations are to behaviourally adapt to changes in frontal systems.

4. This study examines the relationship between frontal systems and the resource acquisition of 64 southern elephant seals during four post-moult and three post-breeding migrations between 2005 and 2010.

5. Satellite-Relay-Data-Loggers provided *in situ* measurements concurrent with >27,500 dive profiles to define fronts and inter-frontal zones between the Subtropical Frontal Zone and the Southern Boundary of the Antarctic Circumpolar Current. For >430,000 *in situ* measurements water mass properties could be identified.

6. Generally, southern elephant seals associate more frequently with more southerly, higher latitude fronts/zones. Body condition improvements related to a given frontal system or water mass vary strongly according to year, season, month and sex.

7. The variability in body condition improvements is higher in some frontal systems than in others, likely due to shifts in the Subantarctic and Polar Front.

8. During a migration, some individuals stay within ≤3 frontal systems, whilst others change between several frontal systems and primarily improve their body condition in upper ocean waters.

9. Southern elephant seals do not trace particular water masses across frontal systems, and both surface and deep foraging strategies are used.

10. This suggests that southern elephant seals do not target particular water mass southern elephant seals but adjust foraging and movement strategies to exploit boundary areas at which mixing and prey aggregation is high.

11. The large behavioural plasticity towards the spatio-temporal variability in the different oceanographic regions they encounter could indicate resilience against environmental changes.

Keywords: Ocean, behaviour, mammals, climate change

1. Introduction

The ocean is currently undergoing dramatic changes in its biological and physical composition induced by anthropogenic climate change. Small increasouthern elephant seals in temperature can lead to large perturbations in the polar regions, thus the Southern Ocean (SO) is one of the most sensitive and vulnerable regions to rapid climate change (Schofield et al., 2010; Trathan, Forcada, & Murphy, 2007). Due to the interconnectedness of the SO with other ocean basins, any perturbations to the SO ecosystem will likely propagate to other areas (Trathan et al., 2007). However, the existing assouthern elephant sealssments of how marine species respond to such environmental changes are inadequate to comprehensively gauge the species-specific vulnerability to these changes (Campagna et al., 2011; Constable et al., 2014; Davidson et al., 2012; Schofield et al., 2010).

The SO's main feature is the Antarctic Circumpolar Current (ACC) which flows clockwise around Antarctica (Orsi, Whitworth, & Nowlin, 1995; Rintoul, Hughes, & Olbers, 2001). Its circulation determines the biological production within its waters as well as the position of oceanographic boundaries (Murphy et al., 2013; Nicol et al., 2000; Pollard, Lucas, & Read, 2002; Rintoul et al., 2001; Talley, Pickard, Emery, & Swift, 2011). The flow of the ACC is concentrated in several fronts, which are characterized by distinct water properties - such as strong current jets, temperature and salinity - by which they can be identified (Sokolov & Rintoul, 2009a). The commonly recognized major circumpolar fronts within the ACC from the north to the south are the Subantarctic Front (SAF), the Polar Front (PF), and the Southern ACC Front (SACCF) (Orsi et al., 1995; Sokolov & Rintoul, 2009a). Outwith the ACC to the north of the SAF lies the Subtropical Front (STF) (Belkin & Gordon, 1996). The water masses within the ACC are mixed and redistributed to the east, with deep waters from the North Atlantic being upwelled at the southern boundary of the ACC following the inclined isopycnals, while mixing with Circumpolar Deep Water (CDW) and, on reaching the surface flow, are diverted northward by Ekman transport (Tomczak & Godfrey, 1994). This newly formed surface water (SW) travels north across the ACC until it reaches the Antarctic Convergence. Here, it mixes with Subantarctic Water from the north and is then subducted to mid-depth, becoming Antarctic Intermediate Water (AAIW), while the ACC carries the water further eastward. Water that is subducted here, but originates mainly from northerly waters is called Subantarctic Mode Water (SAMW). For a schematic of the mentioned fronts, zones and water masses see Talley et al. (2011).

Spatial planning and the designation of protected areas in the SO build upon the identification of important foraging regions. This is because successful resource assimilation ultimately determines the fitness of individuals and reflects the productivity of an oceanographic region. Resource assimilation is thus a valuable metric for measuring the degree to which environmental perturbations can cause habitat shifts and changes in the population dynamics (Costa, Breed, & Robinson, 2012; Miller, Scales, Ingram, Southall, & Sims, 2015; Scales et al., 2014). Understanding the reliance of populations on the SO habitat by long-term monitoring of successful resource assimilation and oceanographic conditions is imperative (Bestley, Jonsen, Hindell, Guinet, & Charrassin, 2013; Murphy et al., 2007). This demands an integrative ecosystem assessment (Levin, Fogarty, Murawski, & Fluharty, 2009), that examines the behavioural responses of marine species in relation to their immediate environment. However, despite the necessity for a better understanding of the SO ecosystem and balancing anthropogenic pressures with conservation needs, ecosystem functioning and resilience are still poorly described and understood (Constable et al. 2014).

Due to the position of southern elephant seals (*Mirounga leonina* Linnaeus 1758) at the top of the food-web, their foraging success and population dynamics impart valuable information about different trophic levels within the SO ecosystem (Charrassin et al., 2009). Southern elephant seals therefore serve as sentinels of change and status of large parts of the SO ecosystem (Constable et al., 2014; Hindell, Bradshaw, Sumner, Michael, & Burton, 2003; Trathan et al., 2007). During their 3-8 month long migrations, southern elephant seals travel through a highly dynamic oceanographic environment, diving within many different water masses, crossing many fronts, foraging within many frontal zones and eddies (Biuw et al., 2010; Boehme, Meredith, Thorpe, Biuw, & Fedak, 2008; Boehme, Thorpe, Biuw, Fedak, & Meredith, 2008; Field, Bradshaw, Burton, & Hindell,

2004; Field, Hindell, Slip, & Michael, 2001; Guinet et al., 2014; Hindell et al., 2003; Jonker & Bester, 1998; Muelbert, de Souza, Lewis, & Hindell, 2013; Van Den Hoff, Burton, Hindell, Sumner, & McMahon, 2002). Oceanic fronts are dynamic narrow boundaries between water masses and currents which separate broader frontal zones, characterized by different stratification (layering of water masses) and productivity (Belkin and Gordon, 1996; Belkin et al., 2009; Orsi et al., 1995). Instabilities along those horizontal fronts can generate eddies with a cyclonic or anticyclonic rotation depending on which side of the front they are emerging (Spall, 1995). Such eddies will exhibit different oceanographic properties than the surrounding water. These dynamic oceanographic features can be short lived, but often are persistent on an intermediate temporal and spatial scale (mesoscale: days to months and 10-100km). Mesoscale eddies, fronts and frontal zones are key to southern elephant seal foraging behaviour, because the physical discontinuities of these oceanographic features serve to aggregate prey (Bailleul, Charrassin, Monestiez, et al., 2007).

Southern elephant seals spend more time in some frontal systems, water masses and eddies than in others (Biuw et al., 2007; Hindell et al., 2016, 2003; Labrousse et al., 2015; Muelbert et al., 2013), likely because foraging along particular fronts or within specific frontal zones is more favourable. Physical cues such as fronts help advect and aggregate prey, leading top predators to respond to these cues for locating the prey (Bost et al., 2009; Fauchald & Tveraa, 2006). Correspondingly, foraging intensity has been shown to increase around mesoscale structures such as eddies at which local productivity is high (Bailleul, Authier, et al., 2010; Bailleul, Cotté, & Guinet, 2010; Campagna et al., 2006; Della Penna, De Monte, Kestenare, Guinet, & d'Ovidio, 2015; Dragon, Monestiez, Bar-Hen, & Guinet, 2010; Massie et al., 2015; Simmons, Crocker, Kudela, & Costa, 2007). Successful resource assimilation can be estimated by a positive change in a seal's buoyancy (Biuw, McConnell, Bradshaw, Burton & Fedak, 2003). This is often used to link foraging success to oceanographic regimes and processes, showing that the return to these specific waters is non-random. Particularly during post-moult migrations, southern elephant seals have been shown to track those water parcels which supported spring blooms upstream (Cotté, D'Ovidio, Dragon, Guinet, & Lévy, 2015). The use of distinct oceanographic regimes with specific temperature and salinity signatures differs for the sexes and is habitat-related, meaning seals adjust their behaviour according to the environment they experience (Bailleul, Charrassin, Ezraty, et al., 2007; Biuw et al., 2010; Campagna et al., 2006; Field et al., 2001; Guinet et al., 2014; Labrousse et al., 2015). However, while the foraging behaviour of southern elephant seals is clearly related to regional oceanography (Biuw et al., 2007; Hindell et al., 2016; Labrousse et al., 2015), individual behaviour does differ. For example, some southern elephant seals use eddies intensively (Cotté et al., 2015), while others do not (Bailleul, Cotté, et al., 2010; Tosh et al., 2015).

Thus far, large-scale and long-term reliance on fronts and frontal zones within the ACC and the adjacent areas for supporting the resource assimilation of southern elephant seals has not been investigated. Currently the relationship between behaviour, distribution and oceanographic processes at spatio-temporal scales relevant to southern elephant seals are unclear and poorly investigated (Cotté et al., 2015). This includes research on how inter-annual changes in oceanographic features such as frontal positions affect the body condition of southern elephant seals. Plasticity in the reliance on specific fronts and frontal zones for improving the body condition could be extremely important for coping with changes in the oceanographic environment due to climate change. Such biological and physical oceanographic changes due to rapid warming are particularly evident now in the region around the West Antarctic Peninsula, but also in other regions of the SO such as the Scotia Sea (Murphy et al., 2013, Schofield et al., 2010). The southern elephant seal populations within the Atlantic sector, and particularly from South Georgia, heavily rely on the West Antarctic Peninsula, the Scotia Sea and the associated shelf-areas for replenishing resources. It is therefore crucial to specifically monitor these populations.

This long-term study addresses this need by relating the (un-)successful resource assimilation of southern elephant seals within the Atlantic sector to the physical oceanographic features which determine the immediate environment they exploit. In particular, the focus of this study lies on a) describing where in oceanographic space and in which frontal systems resources are assimilated; b) assessing whether variations in oceanographic features can explain the spatial and temporal variations in resource assimilation; and c) gauging how flexible the reliance on specific frontal systems is for replenishing resources. This is achieved by combining a suite of new

methods and methodological applications to describe the oceanographic space at the spatio-temporal scale relevant to individual southern elephant seals. Specifically, merging *in situ* oceanographic temperature-salinity data collected by Conductivity-Temperature-Depth Satellite-Relay-Data-Loggers (CTD-SRDLs; Boehme et al., 2009) with ranges of absolute dynamic height measured by satellite altimetry permits inferring the position of seals in relation to the oceanographic fronts. This then allows contextualising the seals' foraging success relative to the frontal systems and corresponding water masses in which the seals dived. The variability of the frontal positions is assessed to gauge its relevance to the seasonal and inter-annual variations in foraging success related to certain fronts and zones.

This multi-faceted assessment of top predator foraging success in relation to the dynamic oceanographic environment permits tracking the inter-annual variability of the SO's ecosystem productivity within the Atlantic sector. The data used within this study spanned several years and seasons, thereby contributing long-term information about many different individuals (see Appendix 1). In combination with the large spatial scale covered by the seals this dataset provides a unique opportunity to assess whether the persistence of specific fronts and the variability of frontal positions influence the resource assimilation. The investigated capability to adapt the movement behaviour to changes in the frontal systems provides valuable insights into the role of southern elephant seals as indicator species of environmental change. The use of this very rich dataset further enables gauging the vulnerability of southern elephant seals towards (climatic) environmental changes at the population level.

2. Materials and Methods

Telemetry data

The data used within this study (Appendix 1) were collected in seven deployments as part of the SEaOS (http://biology.st-andrews.ac.uk/seaos/index.html) and the SAVEX projects (http://www.st-andrews.ac.uk/~savex). As part of these projects, Conductivity-Temperature-Depth Satellite-Relay-Data-Loggers [CTD-SRDLs; Sea Mammal Research Unit (SMRU) Instrumentation, St Andrews, UK] were deployed on 64 southern elephant seals on the islands of South Georgia, South Atlantic, and the Falkland Island, South Atlantic, between the Austral summer of 2005 and the Austral summer of 2010. The capture and tagging protocols were reviewed and approved by the University Teaching and Research Ethics Committee (UTREC) and the Animal Welfare and Ethics Committee (AWEC) as part of the ethical review process and were scrutinized under the UK Animal (Scientific Procedures) Act 1986. Capture and deployment of satellite transmitters was carried out by experienced personnel with UK Animal (Scientific Procedures) Act 1986 Personal Licences.

In total, the CTD dataset of these seven deployments comprised 27,638 unique CTD profiles. The CTD dataset provided hydrographic information collected during the ascent of the deepest dive within a 6-hour summary period (Boehme et al., 2009). Initially, CTD measurements were taken at a 1 Hz sampling frequency. For satellite-transmission via the Argos system, each high-resolution CTD profile was reduced to a CTD profile which constituted 17 conductivity, temperature and pressure measurements. These were chosen according to predefined depth criteria and the broken-stick algorithm (Boehme et al., 2009).

In the following, the telemetered information from the SRDLs was used which provided broken-stick abstracted dive profiles with four at-depth and two surface dive inflection points (Fedak, Lovell, & Grant, 2001; Photopoulou, 2012) and the corresponding *post hoc* calibrated CTD data (Roquet et al., 2013) which were made freely available by the International MEOP Consortium and the national programmes that contribute to it (http://www.meop.net). Since the amount of data that can be transmitted via telemetry is restricted, only a random selection of all high-resolution profiles collected by the SRDLs were abstracted, transmitted and received (Fedak, Lovell, McConnell, & Hunter, 2002; Photopoulou, 2012).

The CTD data were imported into Ocean Data Viewer (Schlitzer, 2015) and the potential temperature (Θ), the potential density (ρ_θ) and the neutral density (γ_n) were calculated for each CTD measurement from the *in situ* temperature, salinity and pressure measurements. There were no salinity recordings in the CTD dataset for seven individuals (ct8-26632-05, ct8-17221-05, ct45-22482-08, ct58-1548-09, ct58-48927-09, ct58-48923-09, ct65-9043856-10); hence Θ, ρ_θ and γ_n could not be calculated for these individuals. The resultant extended CTD dataset was exported and re-imported into the programming software R (R Core Team, 2013) for further analysis.

Satellite altimetry data

To improve the localization of oceanographic zones, sea surface heights and their anomalies inferred from the absolute dynamic topography were used to allow distinguishing oceanographic features and investigating their variability. The absolute dynamic topography estimates, measured in dynamic metres (dyn m), were obtained from delayed time mode satellite altimetry products distributed by Aviso (http://www.aviso.altimetry.fr). These products were derived from the Ssalto multi-mission ground segment (Ssalto)/Data Unification and Altimeter Combination System (Duacs) processing (Aviso, 2016). The Ssalto/Duacs system integrates the satellite missions of HY-2A, Saral/AltiKa, Cryosat-2, OSTM/Jason-2, Jason-1, Topex/Poseidon, Envisat, GFO, ERS-1 and ERS-2. The resultant satellite products are consistent and homogenized. Maps of absolute dynamic topography are obtained by the sum of the mean dynamic topography (MDT) and the surface level anomaly (SLA) relative to a 20-year reference period (Aviso, 2016). More specifically, daily maps of absolute dynamic topography from Aviso's Ssalto/Duacs two-sat merged MADT-H global sea surface height product (1/4°x1/4° resolution on a Cartesian grid) were used in this analysis (Aviso, 2016). For further information on this product, please see Aviso (2016) and Boehme, Thorpe et al. (2008). The absolute dynamic topography value of the grid cell closest to each recorded latitudinal and longitudinal position was extracted for each CTD profile along each trajectory. Dynamic height measurements could not be obtained for the location and datetime of 107 unique CTD profiles. Daily maps of SLA height, measured in m, were obtained from AVISO's Ssalto/Duacs all-sat merged MSLA-H global sea surface height product with a 1/4°x1/4° resolution on a Cartesian grid (Mertz, Rosmorduc, Maheu & Faugère, 2016). The SLA variance for each grid cell was calculated over a 7-day sliding window. The SLA variance value of the grid cell closest to each recorded latitudinal and longitudinal position were extracted for each CTD position along each trajectory.

Assigning oceanographic classifications

Following the methodological approach of Boehme, Meredith et al. (2008), the distribution of the Southern Ocean fronts was defined on the basis of *in situ* potential temperature ranges (Table 1) to account for the mesoscale, dynamic variability of their position. From north to south, the resultant fronts and zones were: Subtropical Zone (STF), Subtropical Front (STF), Subantarctic Zone (SAZ), Subantarctic Front (SAF), Polar Frontal Zone (PFZ), Polar Front (PF), Antarctic Zone (AAZ), Southern ACC Front (SACCF), Southern Zone and the southern boundary of the ACC (SB). Ranges south of and including the SAZ were derived from Boehme, Meredith et al. (2008), while the ranges for the STZ and the STF were chosen according to Orsi et al. (1995).

The front or frontal zone was determined by following changes in temperature at a given depth or depth range (Suppl. Figure 1). This required CTD measurements at 500 m for regions south of the PF and at 300m for regions between the SAZ and the PF. However, seals often did not dive deeper than 200 or 300 m during a six hour period in which a CTD profile was taken. Thus, dives with such shallow CTD profiles could only be assigned to one of two generic groups covering (a) the SAZ to PFZ or (b) everything south of the PF. Using the specified potential temperature ranges, the whereabouts of each individual could be determined in an oceanographic sense (Table 2). For 32% of the CTD profiles the position could only be specified as either 'south of PF' or 'SAZ to PFZ'. However, 13 % of the CTD profiles were too shallow or outside the specified potential temperature ranges, leaving the positioning of the seal in this oceanographic sense unidentifiable.

Those positions that could be defined in oceanographic space mapped well against the average fronts (derived from Boehme, Meredith et al. (2008)) presented in geographic space (Suppl. Figure 2). Using *in situ*

temperature data to define the fronts also enabled to see when individuals were diving within eddies (Suppl. Figure 2); because when seals dived within eddies, the front or zone indicated by the outlined method did not match the frontal system of the spatial-temporal surrounding.

Absolute dynamic topography ranges for each front and zone were devised by incorporating the inferences made from the *in situ* potential temperature data. Each CTD profile was assigned to a front or zone based on potential temperature. On the basis of this categorization, five number summary statistics (minimum, 1st/2nd/3rd quartile, and maximum) of absolute dynamic topography were obtained for each front or frontal zone. The data were not normally distributed and therefore non-parametric statistics were used to find ranges of dynamic height for each front and frontal zone. Venables, Meredith, Atkinson, and Ward (2012) indicated seasonal differences in the absolute dynamic topography ranges. To resolve the position in oceanographic space at the spatial and temporal resolution relevant to the seals, separate ranges for each season and year were chosen. Five-number summary statistics of dynamic height were calculated for each front/zone in each season (winter/summer) of each year. Primarily the 1st and 3rd quartiles were used to draw the ranges. The final ranges were determined by comparing the width of the inter-quartile-ranges, potential overlap with other zones or fronts and the density of data which informed on the dynamic height ranges (Table 3). If no summary information could be obtained for a given front/zone, but data from the adjacent fronts/zones were available, then the dynamic height range for this front/zone was defined by the minimum or maximum dynamic height value of the adjacent zone/front. However, when there was no information on two adjacent zones/fronts, no dynamic height ranges could be defined for the zones and fronts in question (e.g. SACCF and SB in summer 2010).

Many CTD profiles could not be assigned to fronts with either the potential temperature or dynamic height approach alone, so both approaches were combined. This merged approach allowed the majority of CTD profiles to be assigned to a front or frontal zone, rendering a dataset of the best available resolution. The altimetry measurements covered a larger spatial domain, yet the data were spatially and temporally smoothed. This meant that the dynamic height measurement of the grid cell closest to a seal's position only provided an approximate estimate of the real dynamic height at that given place and time. This diminished fine-scale variations that show sudden changes in oceanographic properties or the presence of short-term persisting eddies. Contrastingly, the temperature data were recorded *in situ* at the same spatio-temporal scale as the seal movement data revealing these fine-scale variations. Therefore, temperature ranges were deemed more reliable than dynamic height for defining fronts. If the oceanographic positioning of a seal at a given time point could be assigned using either *in situ* potential temperature or dynamic height, the result obtained on the basis of potential temperature was retained. When a CTD profile could only be assigned by one approach, its respective result was taken. In the case that insufficient temperature information was available so that a CTD profile could only be assigned to the two generic groups 'SAZ to PF' and 'south of PF', the result of the dynamic height method was taken insofar as this result was consistent with the generic groups. In other words, if a measurement was initially assigned to the 'SAZ to PF' group, then the result of the dynamic height method was only retained if this approach suggested that the respective CTD profile was in the SAZ, the SAF or the PF. Merging the results of these two approaches did not only result in having fewer unclassified positions, but it also enabled to further detail the oceanographic position of dives ascribed to the two generic groupings 'SAZ to PFZ' and 'south of PF'.

For each location, the water mass for a given CTD profile was determined. Water masses were defined on the basis of neutral density ranges for the Atlantic sector of the Southern Ocean (Table 4) (Arhan, Naveira Garabato, Heywood, & Stevens, 2002; Herraiz-Borreguero & Rintoul, 2011; Heywood & King, 2002; Muelbert et al., 2013). The frontal ranges were determined using the merged approach and the CTD measurements assigned to specific water masses were recorded. Individual variation in the amount of time spent at the bottom of a dive for a given water mass was determined relative to their maximum dive depth, and in relation to both sex and sex/ seasonal differences.

Heat maps were produced to assess whether individuals would trace certain water masses as they crossed fronts and into frontal zones in which the layering of water masses differed to that of the previous zone. These heat maps depicted how frequently individuals were in a given water mass (overall and at their maximum dive depth)

when in a given front. Transitions from one preferred water mass in one frontal system to another water mass in another frontal system were also investigated with regard to sex and season (post-moult and post-breeding).

For the reason that CTD profiles were taken in almost regular 6-hour intervals, the percentage of time a seal spent in each front or zone during its entire migration could be derived. For this, the frequency of each individual being in each frontal system, determined by the merged approach, was divided by the total amount of unique CTD profiles recorded for each individual. Pooling the data of all individuals, the amount of time spent in each frontal system was examined for sex and seasonal differences. Time series of the frontal system in which individuals were in at a given time point revealed inter-individual temporal patterns. To relate these patterns to geographic space, the trajectories of all individuals were coloured according to which frontal system the animal was in at that given date-time.

Relationship between frontal systems and southern elephant seal behaviour

To link the productivity of an area to the prevalent oceanographic features, the resource acquisition and thus foraging success of southern elephant seals can be indirectly estimated by examining body composition changes (Biuw et al., 2007, 2003; Robinson, Simmons, Crocker, & Costa, 2010). These can be detected from the rate at which an individual sinks or rises during passive drift phases, i.e. an individual's buoyancy (Biuw et al., 2003; Crocker, Le Boeuf, & Costa, 1997). The buoyancy change data used in this study resulted from the identification of drift phases with a step-wise filtering method (Gordine, Fedak, & Boehme, 2015). For 64 southern elephant seals, the time series of the drift rates extracted by the filtering method were visually inspected for apparent trends in buoyancy changes. Some of the drift rate time series showed discontinuities in the trends; while in other cases the step-wise filtering method rendered unclear results for detecting buoyancy changes. Thus, as suggested by Gordine et al. (2015), the selection criteria for some individuals were altered by visually inspecting the respective drift rate time series after adjusting each selection criterion one at a time. For the reason that many of the selection criteria are linked to each other and work in concert, e.g. fragment length and dive duration, this adjustment and visual inspection process was iterative and in some cases was performed multiple times. In some cases, a given selection criterion was removed if it was found to be ineffective. When an animal supposedly approached or reached positive buoyancy or hauled-out, the drift rate time series was subdivided into pre and post haul-out and pre and post positive buoyancy sections and manual adjustments of selection criteria were performed for each section separately. Afterwards, the drift rate time series sections were joined again to obtain one time series per individual. Lastly, any outliers remaining in the adjusted time series were manually removed. For a detailed list of all adjustments to the selection criteria and the removal of outliers for each individual see Gordine (2017).

Subsequently, a cobs spline was fitted to the resultant time series of each individual to provide representative drift rate estimates (Gordine, 2017; Gordine et al., 2015). The drift rate was predicted for each individual by evaluating the relevant cobs algorithm at each CTD profile's date-time point. Drift rate information was unavailable for four individuals (ct40-48926-08, ct40-22490-08, ct49-92568-09, ct65-22496-10). Since the CTD profiles were not necessarily taken during drift dives, the information about drift rate had to be interpolated from each individual's predictive drift rate spline. Often CTD profiles were still recorded long after the last drift rate information was available. This led to extrapolated drift rates associated with a CTD profile beyond what could be expected. Hence all predicted drift rates below -0.6 $msec^{-1}$ and above 0.25 $msec^{-1}$ were set to this minimum and maximum level based on the previously published ranges (Biuw et al, 2003, 2007; Gordine et al., 2015). The mean predicted drift rate was calculated for each day, smoothing out slight temporal variations in drift rate. The difference in the mean predicted drift rate of one CTD profile to the next CTD profile was calculated ($\Delta drift.rate_n$). Finally, this difference was then divided by the temporal daily difference of one CTD profile to the next (Δt_d) to obtain the daily change in drift rate ($daily\Delta drift.rate_n$).

$$daily\Delta drift.rate_n = \frac{\Delta\, drift.rate_n}{\Delta t_d} \qquad [\text{in } msec^{-1}d^{-1}]$$

where

$$\Delta drift.rate_n = drift.rate_n - drift.rate_{n-1}, \quad for\ n > 1 \qquad [\text{in } msec^{-1}]$$

and

$$\Delta t_d = t_d - t_{d-1}, \quad for\ n > 1 \qquad \text{[in days } (d)\text{]}$$

Boxplots were used to discern any relationship between daily drift rate changes and fronts/zones. For this, the daily drift rate changes were related to where in oceanographic space the individual was. To determine whether there were any long-term trends in body condition improvement associated with specific frontal systems, those data were separated according to season (post-moult and post-breeding) and year. For the reason that the majority of data were collected in the post-moult and post-breeding season of 2008 and 2009, monthly comparisons between these years could be made for post-moult and post-breeding migrations respectively. Furthermore, through combining the data of all individuals in each season and year, the median daily change in drift rate could be obtained for each frontal system. This was used as an indicator for how successfully an individual assimilated resources in a particular front or zone during a particular year and season. It allowed a comparison of long-term changes in the body condition of southern elephant seals in relation to each frontal system.

The information on oceanographic positioning in terms of frontal system and water mass at the maximum dive depth was combined with the information on body condition. This allowed assessing whether particular water masses with respect to the layering of water masses in given frontal systems supported body condition improvements more than other water masses within the same frontal system or the same water mass in a different frontal system.

Heat maps showing the median daily buoyancy change indicated in which water masses and in which frontal systems individuals experienced on average a positive drift rate change. Individuals were further subdivided into two groups – locals and roamers – depending on how many frontal systems they crossed during their migrations. 'Locals' primarily stayed within a maximum of two frontal zones and crossed up to two fronts at the most; 'roamers' were found in more than four different frontal systems (Table 5). It was investigated whether there were any differences between 'locals' and 'roamers' regarding water masses within given fronts and daily drift rate changes. This three-way interaction between frontal systems, water masses and body condition was also examined with regard to sex and seasonal differences.

3. Results

Using potential temperature to define an individual's position in terms of fronts and frontal zones was successful for 88 % of all unique profiles and 57 % could be assigned to a specific front or frontal zone (Suppl. Figure 3). A more general definition of the position (SAZ to PF and south of PF) could be assigned to 36 % of the profiles for which the CTD profile were not deep enough to allow a more specific definition. Merging of the potential temperature and the dynamic height approaches often allowed such CTD profiles to be further defined. The results in relation to oceanographic fronts presented below were obtained with the merged approach, because this generally provided more details on the positioning of seals. How much time each individual spent in each fontal system varied greatly according to the individual (Figure 1). On average, seals visited 3-4 different frontal systems during a migration and there was large individual variation in which fronts and zones seals dived. However, there was no long-term pattern of certain fronts or zones being more recurrently visited than others during certain years and/or seasons. Overall, seals were most frequently in the SB (Table 2). Individuals were also frequently located in the AAZ and the PFZ. Generally, the southernmost fronts and zones were more heavily targeted than the northern frontal systems. Seals spent least of their time in the actual fronts (STF, SAF, PF, SACCF), but were rather found in the frontal zones. However, if individuals were found within fronts, then they were most often found in the SACCF.

The amount of time spent in each frontal system varied by season. During post-moult migrations, females were most frequently in the SB; while post-breeding females were more often in the AAZ (Figure 2). Overall, post-moult males spent more time in the PFZ and the AAZ and less time in the SAZ and SB than post-moult females

(Figure 2). In terms of how much time individuals spent in each frontal system, the behaviour of post-moult males appeared to become more similar to that of post-breeding females. Although the time spent in each frontal system depended both on season (χ^2 =1866.719, df =8, p<0.001) and sex (χ^2 =308.827, df =8, p<0.001), the seasonal differences appeared to be larger than the sex differences. Inter-individual differences in how many and in which fronts individuals were during a migration were large (Suppl. Figure 4). The amount of time spent in each frontal system depended on the individual (χ^2 = 37878.160, df = 460, p < 0.001). While at the beginning and the end of migrations many fronts and zones were crossed, some individuals spent the mid-portion of the migration in primarily one or two zones.

Since the foraging success of southern elephant seals reflects the availability of prey, the monitoring of buoyancy changes provided a good seasonal and inter-annual assessment of ecosystem productivity.The daily drift rate change was generally positive, but frontal systems in which seals had the biggest positive increases in buoyancy varied strongly across the years and seasons (post-moult and post-breeding) (Figure 3), but also during seasons (Suppl. Figure 4 & 5). Overall, there was a stark difference between the post-moult and the post-breeding trips, with a generally larger positive daily drift rate change during the post-breeding season (Figure 3). While the variability for the more southern zones south of the PF was high during both seasons, the zones north of the SAF showed higher positive changes during the post-breeding season compared to the post-moult trip. The same is true for the PF as an only average or below average region for increasing buoyancy during the 2008 and 2009 post-moult migrations; whereas during the post-breeding migrations of the same years being in this front led to a highly positive daily change in buoyancy (Figure 3).

One long-term temporal shift for the post-moult migration was apparent. For the post-moult migration, the daily drift rate change for the zones north of the SAF was decreasing from positive values in 2005 to even negative values in the 2009 post-breeding season. For the post-breeding migration, the variability of the daily drift rate change for the zones south of the SAF between 2008 and 2009 was very different, with some seals experiencing highly positive drift rate changes in 2009 (Figure 3). During the post-breeding migration in 2009, seals showed a very negative daily drift rate change for the SAF (Figure 3), which is not seen at any other time. Such sudden shifts between areas in which seals achieved positive and negative buoyancy changes, lead to the question of whether these patterns can be explained by shifts in the dynamics of fronts and zones. The variances in SLA associated with the AAZ, the PFZ and the SAZ increased from 2005 to 2010, indicating higher variability in the water column structure within the same front or zone. (Suppl. Figure 7). Contrastingly, the variances in SLA variance for the southernmost fronts and zones (SACCF and SB) were more stable over the years. This coinciding change in the areas supporting the strongest resource gains and the increase in variability of the fronts indicates that increased variability in the water column structure had negative effects on the resource gain. However, in the SAZ and PFZ the SLA variance were very low in December 2009 compared to the rest of the year (Figure 4). The low variance in SLA variance in the PFZ in December 2009 (Figure 4) also indicates a very consistent structure of the SAF. The particularly low value in the variance in the SAZ is most likely the results of very few mesoscale features (like meanders and eddies) disturbing this zone. Correspondingly the daily drift rate change was lower compared to the previous year when the variance was higher. Contrastingly, the PF and AAZ showed comparatively higher variances in December 2009 and a higher associated resource gain. Overall, this indicates that some variability in the water column structure, e.g. through eddies aggregating prey, is required to achieve resource gains. However, too much variability in the water column is less favourable in terms of resource gain compared to more stable conditions as exhibited e.g. by the SACCF and SB

Over 85 % of CTD measurements were identified as belonging to specific water masses (Table 6). Despite individuals having been in the right geographic and oceanographic space for encountering SAMW, none of the CTD measurements had the matching characteristics (Table 6). The most frequently encountered water mass was SW. One measurement was taken in WSBW; however none of the measurements matched the characteristics of WSDW or AABW. Between the SAZ and SB, most LCDW was high in salinity. The variety of different water masses frequently encountered by southern elephant seals increased with latitude. Water masses in the upper ocean layers (SW, AAIW, UCDW) were more frequently visited than those at the bottom. The mid and bottom layers were only frequently visited in the SB. The only exception to this was the low saline

LCDW1 mid-ocean layer which was frequently encountered in the PFZ by two individuals. In the SB, individuals were almost as frequently in mCDW as in SW, and also often in mSW. These apparent trends for the SB roughly applied to the generic grouping 'south of PF' as well. However, when looking at how frequent certain masses could be found at the bottom of dives, slightly different patterns became apparent. In the SB, individuals were most often in mCDW at the bottom of their dives. Being in SW at the bottom of dives was also more common than being in LCDW; while both of these water masses were encountered much more frequently than any of the other water masses. In the SACCF, the AAZ and the PFZ individuals were in UCDW at the bottom of their dives. AAIW was also relatively frequently found at the bottom of dives north of the AAZ.

The time individuals spent in each water mass differed according to sex ($\chi^2 = 695.401$, df = 6, $p < 0.001$). Females and males spent about equal amounts of time in SW and UCDW (Figure 5). However, females spent more time in AAIW and less time in mCDW than males. Males also spent more time in LCDW and the higher salinity LCDW2. Within the SACCF, the PF, the SAF and SAZ females spent marginally more time in surface waters than males (Suppl. Figure 8). The largest differences could be found within the SB. Here, both females and males were most frequently in mCDW next to SW. However, females were overall more frequently in mSW and LCDW than males and also dived in ISW, which none of the males did. At the bottom of dives, females encountered a larger variety of different water masses than males. North of the AAZ, females were more often in AAIW at the bottom of their dives compared to males.

There were hardly any qualitative differences between the seasons in the amount of time individuals spent in each water mass within a given frontal system (Suppl. Figure 9). The major difference was the lack of mSW, and ISW being less frequently encountered during the post-breeding migrations. During post-breeding, individuals were more often in SW at the bottom of their dives. Seasonal differences in the amount of time individuals were within given water masses were linked to the sex differences (Figure 5) and the proportion of time each individual spent in a given water mass depended on the season and sex ($\chi^2 = 1870.330$, df = 12, $p < 0.001$). Females spent roughly the same amount of time in SW and AAIW in both post-moult and post-breeding seasons. However, during the post-breeding period, females spent much more time in UCDW and less time in mCDW. During post-moult migrations females spent similar amounts of time in mCDW as males. However, only males seemed to encounter the higher salinity LCDW2 found south of the SAF and north of the SB.

As with the fronts, there was large inter-individual variation over time in which water masses were found at the maximum dive depth (Suppl. Figure 10). However, individuals that were in mCDW at the bottom of their dives returned to depths at which mCDW was present for extended time periods. This trend was linked to staying within the same frontal system, particularly the SB (Suppl. Figure 10). Those individuals that primarily encountered AAIW and UCDW at the bottom of their dives frequently changed between these two water masses and also SW. This alternating pattern was, however, not necessarily reflected by changing between frontal systems. Thus, it appears that some individuals alternated between one, two or three preferred water masses within and across frontal systems. However, individuals did not consistently trace particular water masses across fronts.

Frontal systems, water masses and body condition

Looking at the oceanographic positioning of individuals in relation to their body condition indicated which frontal systems and, within that, which water masses likely provided the necessary resources to support body condition improvements (Figure 6). Generally, individuals in water masses associated with fronts and zones north of and including the PF displayed a stronger body condition improvement. Within the PF, the low salinity LCDW1 stands out as a water mass which provided resources for strong body condition improvements. SW in the STF was the least favourable oceanographic region. However, pooling the data of all years and individuals, it did not appear as though any particular water mass in a particular frontal system was substantially more favourable. These trends only became apparent by looking at sex, seasonal and movement differences.

Firstly, by looking at the mean daily drift rate changes of 'locals' versus 'roamers' revealed that particularly the upper ocean layers (SW, AAIW and UCDW) in the PFZ, SAF and STZ were really favourable oceanographic

regions for 'roamers' (Figure 6). Contrastingly, SW in the STF and SAZ, but also in AAZ and SACCF was not a favourable water mass to be in for 'roamers'. On the other hand, the body condition of 'locals' generally seemed to vary less strongly across regions. 'Locals' primarily improved their body condition in LCDW2, but also in other derivatives of CDW. An exception here was within the SB, in which the surface layers appeared to be more favourable for 'locals' than the deeper layers. Interestingly, for 'roamers' this relationship in the SB was reversed.

In terms of sex, females generally appeared to experience stronger positive increases in drift rate change than males. Males primarily improved their body condition when they were in SW at the bottom of the dives within the AAZ and the SB. On the contrary, females did poorly in this water mass within these two fronts. Females particularly thrived when being in SW and AAIW at the bottom of their dives within the STZ and SAF. For females, LCDW1 within the PF was a water mass in which individuals experienced a sustained increase in drift rate. Generally, the derivations of CDW in the more southern fronts and zones supported body condition improvements in females. There was a latitudinal trend with regards to AAIW and UCDW at the bottom of dives, with higher body condition improvements occurring more towards the northern frontal systems. This trend was similar for both males and females, but males generally did more poorly in these waters than females.

During the post-breeding migrations, whenever individuals were within LCDW1 – but in particular in the PF - they tended to experience strong body condition improvements (Figure 7). Generally, individuals who were in the derivatives of LCDW at the bottom of their dives and south of the SAF improved their body condition at a faster rate compared to water masses in the upper layers. Within frontal systems north of the PF, SW and AAIW were water masses in which body condition greatly improved during the post-breeding period. During the post-moult migrations, individuals in these regions only experienced slight body condition improvements. The only water mass in which individuals experienced a stronger improvement in body condition was AAIW within the SAF. Body condition improvements were roughly equal in the post-moult period among the remaining frontal systems and water masses. Only SW in the STZ stood out as a particularly unfavourable region.

4. Discussion

The results demonstrated that southern elephant seals associated more frequently with more southerly, higher latitude fronts/zones within the ACC. The body condition improvements related to a given frontal system or water mass varied strongly according to year, season, month and sex. Despite this high variability, improvements in body condition were higher in some frontal systems than in others, and generally occurred at a faster rate during the post-breeding migrations compared to the post-moult migrations. This indicates higher productivity during the post-breeding migrations coinciding with the Austral spring and summer, emphasising the usefulness of monitoring buoyancy changes as a means for assessing seasonal and inter-annual ecosystem productivity. Furthermore, the data revealed high individuality, and both inter-individual and intra-individual variation in the use of frontal systems was evident. These results respectively suggest that southern elephant seals do not target particular water masses but adjust foraging and movement strategies to exploit boundary areas at which mixing, and prey aggregation is high. Southern elephant seals adjusting their behaviour and movement accordingly manifests large behavioural plasticity towards spatio-temporal variability in the different oceanographic regimes they encounter.

Presence in different frontal systems

The time spent in particular frontal systems strongly differed between individuals (Figure1), illustrating the high inter-individual variability. Yet, southern elephant seals spent generally more than 60% of their time south of the PF (Figure 2). However, the importance of this has to be put into context. Firstly, the breeding and moulting sites on South Georgia of this population lie south of the PF and therefore large parts of the migrations need to be within these oceanographic regimes by necessity. That has to be taken into account when interpreting the data. Secondly, the requirement for seals to dive below 500 m within a 6-hour summary period to fully resolve

an individual's position in oceanographic sense was not always met. Depending on the season, oceanographic regime and sea ice concentration, diel dive variation can be very high (Biuw et al., 2010; Guinet et al., 2014). This is particularly true for more poleward colder regimes and during post-moult migrations (Vacquié-Garcia, Guinet, Laurent, & Bailleul, 2015). Therefore, diel dive variation could lead to a potential bias, as an individual's position is more likely to remain undefined during the night and when an individual is in more southern frontal systems of the ACC. This is particularly important because the CTD profiles only provide a snapshot of an individual's position every 6 hours. Small-scale changes, for example when an individual briefly crosses or stays within a front, are thus unlikely to be captured. On the contrary, if an individual stayed within a front for an extended period, this would be captured and is thus an indicator of an individual's association with a given front. Overall, the variation in the amount of time each individual spent in certain frontal systems was high across the seasons.

Individuals spent more time in the SB and subsequently less time in the AAZ during post-moult migrations compared to post-breeding migrations. However, few individuals moved towards the Weddell Sea where the sea ice extends far north. Rather, many individuals moved in the direction of the Antarctic Peninsula. So, the large amounts of time spent in the SB during the post-moult migrations were likely spent in the SB close around the shelf edge along the northern tip of the Antarctic Peninsula. While in this study the proportion of time spent in the adjacent PFZ was similar for males and females, it was apparent that males spent less time in the northern frontal systems. Males in particular spent more time compared to females in the SB and AAZ in shelf-waters around the coastlines of the Antarctic Peninsula and the southern islands of the Scotia Arc. Males have been reported to forage more commonly in shelf-waters (Hindell et al., 2016). Thus, this could be a likely explanation for this sex difference. Also, males from the Macquarie Island population tend to improve their body condition more in areas south of the PF (McIntyre, Donaldson, & Bester, 2015).

Individuals classified as 'locals' were primarily tracked during post-moult migrations and exhibited long periods in which they stayed within one given frontal system, which was very often the SB. So, the differences in the amount of time spent in the SB between post-moult and post-breeding migrations could, in part at least, be attributed to the particular behaviour of 'locals'. However, it did not explain why these individuals primarily targeted the SB. One obvious explanation would be the availability of prey. Interestingly, within the SB both SW and mCDW were most frequently found at the bottom of dives. This suggests that individuals likely employ two alternative foraging strategies within this zone, indicating intra-individual variability and hence plasticity in the behaviour. It has been suggested that particularly males forage at the surface for Antarctic silverfish (*Pleuragramma antarcticum* Boulenger 1902) during winter when the light levels are low (Labrousse et al., 2015). While this may explain the frequent return to SW, both males and females were more often in mCDW at the bottom of their dives. So, individuals most likely target another prey type - possibly myctophids (*Gymnoscopelus nicholsi* Gilbert 1911) - by frequently diving to depths at which mCDW can be found. In our area of study, the SB follows the shelf break along the Antarctic Peninsula and the southern Scotia Arc, which is often associated with higher Antarctic krill densities (Silk et al., 2016). Antarctic krill is a major food source for other mesopelagic fish, which in turn is another prey for southern elephant seals (Cherel, Ducatez, Fontaine, Richard & Guinet, 2008; Saunders, Collins, Stowasser & Tarling, 2017). Therefore, the SB within the Scotia Sea is potentially a very favourable region for southern elephant seals foraging, and the SB was a feature in which individuals generally improved their body condition (Figure 3). Therefore, the SB consistently appeared to be a favourable region overall, and is likely to become more favourable as the SACCF shifts southward. Furthermore, the SB includes important shelf habitats *inter alia* along the Antarctic Peninsula. This is a vulnerable region because of the rapid warming due to warming due to climate change (Schofield, et al. 2010). So the SB is a significant and meaningful target area for management and conservation.

Body condition changes in relation to frontal variability

In this study, the PF and the PFZ were overall areas in which individuals improved their body condition with strong inter-annual, seasonal and monthly fluctuations in the profitability of this front and zone (Figure 3). This seasonal variation could be linked to the seasonal poleward shift of the PF during the austral summer-autumn and vice versa (Freeman, Lovenduski, & Gent, 2016; Kim & Orsi, 2014; Shao, Gille, Mecking, & Thompson,

2015). Interannual variability can play a role as well. In 2008 the PF was positioned further south than during 2009 (Freeman et al., 2016; Kim & Orsi, 2014), which could explain the variability in the daily drift rate change during the 2008 post-moult migration and the stronger seasonal trends during the 2009 post-moult migration. This would therefore indicate that a more poleward positioning of the PF is favourable. Indeed, despite the large inter-annual variability, the average trend in the past years has been towards a slight poleward positioning of the PF (Kim & Orsi, 2014). In January 2010 these two frontal systems also supported improvements in body condition, whilst in the previous year the PF and the PFZ were bad regions for achieving the latter. Although approaching the summer, the position of the PF would have shifted poleward and thereby making the PF and the PFZ favourable foraging zones, the inter-annual overall northward shift of the PF in 2009 may have masked this effect. In 2010 the seasonal shift in the PF coincided with the inter-annual poleward shift of PF (Kim & Orsi, 2014), potentially strengthening the favourable conditions in the PF.

This could explain the strong seasonal trends and their variability regarding body condition changes during the 2009 post-breeding migrations. Overall, the seasonal variability in the PF position is most pronounced over deep ocean basins where there is no topographic steering of the fronts (Dong, Sprintall, & Gille, 2006; Boehme, Meredith, et al., 2008; Freeman et al., 2016). Two such areas are located between 45°-50°S 0°-30°W and 60°S 90°W-70°S 90°W (Freeman et al., 2016) and southern elephant seals in this study were frequently active in both of these areas. Thus, these seasonal shifts could be highly relevant for explaining variability in body condition improvements associated with the PF and the PFZ. This latitudinal position of the PFZ might also play a role as to why southern elephant seals from Marion Island do not forage successfully in very northward waters of the PFZ (McIntyre et al., 2015), while the more poleward PFZ further east is an important region for some females and juvenile males from the Kerguelen Islands (Bailleul, Authier, et al., 2010). However, most individuals from the Kerguelen Islands spend their time in frontal systems south of the PF (Guinet et al., 2014) and improve their body condition whilst foraging along the PF (Bailleul, Charrassin, Monestiez, et al., 2007).

Similar seasonal variation in body condition changes as described in relation to the PF and the PFZ could be seen regarding the AAZ. Concurrent with the seasonal poleward shift of the PF, body condition in the AAZ improved at the end of spring until the end of summer and we also see a generally positive trend towards the AAZ becoming a more favourable region. The AAZ sits between the PF and the SACCF and both displayed a poleward shift over the years and in the area of this study (Kim & Orsi, 2014; Sokolov & Rintoul, 2009b) from which the southern elephant seals seemed to benefit. Interestingly, several studies on southern elephant seals (primarily from the Kerguelen Islands) found that body condition worsened, and prey capture attempts decreased particularly when individuals were in the AAZ (Biuw et al., 2007; Guinet et al., 2014; Labrousse et al., 2015). It can thus only be explained by reduced productivity associated with this zone in this part of the ocean compared to the region presented here (e.g. Deppeler & Davidson, 2017).

The SAF is a very persistent feature, which is topographically constrained particularly along the northern Scotia Arc. The SAF displayed inter-annual variability in its positioning with a slight long-term poleward shift similar to the SACCF and the PF (Kim & Orsi, 2014; Shao et al., 2015), but without any seasonal shifts (Shao et al., 2015). While individuals spent very little time within the SAF, southern elephant seals showed very positive daily drift rates improving their body condition irrespective of the year or season. The only exception being during the post-breeding trips in 2009, when the SAF was highlighted as the only region in which daily buoyancy changes were strongly negative. This finding is fully based on the seals' positions in the SAF being identified with the dynamic height method with only few data points available. However, while the SLA variances generally increased over time, the variance in SLA and its variability (including maximum values around the SAF) during the post-breeding 2009 migrations were exceptionally low when compared to other times (Figure 4). This indicated few changes of the SLA along the SAF, i.e. few mesoscale features. While our method of comparing *in situ* temperature readings to the surrounding area does not provide as detailed information on the association of southern elephant seals with eddies as other more refined approaches do (Bailleul, Authier, et al., 2010; Campagna et al., 2006; Dragon et al., 2010; Massie et al., 2015), it allowed for the determination of when individuals dived within eddies or meanders with other oceanographic regimes around them. At least 29 individuals were swimming in direct association with such features with 18 of them

being also classified as 'roamers' indicating that it was generally common for southern elephant seals irrespective of their foraging strategies. Visually identified eddies in the PFZ had often the oceanographic characteristics of stemming from the SB (cold-core eddies), which are often associated with higher productivity. Several consecutive CTD profiles with this same signature indicated that animals were tracing eddies (Suppl. Figure 11). However, there was little evidence that individuals stayed in association with eddies for longer than one or two sampling periods, i.e. 12 hours. Nevertheless, the correlation between the low SLA variance and the negative drift rate change during the post-breeding trip in 2009 indicates that a lack of such cold-core eddies can have a negative impact on the body condition of southern elephant seals.

Southern elephant seals in the Atlantic sector frequently went to the Patagonian shelf and north of the Falkland Ridge, thereby being in waters of the SAZ and the STF. Generally, these northern fronts and zones were areas in which seals improved their body condition. However, as of the 2009 post-breeding migration the SAZ became a less profitable region. This trend was perpetuated through to the STF, which was particularly bad for improving body condition in the 2010 post-moult period. These trends could relate to the southward shifting of the SAF as well as shifts in the STF positioning (Kim & Orsi, 2014). However, it can also stem from population differences, because the 2010 data was based on individuals from the Falkland Island opposed to South Georgia residents.

The general locations of the SAF, PF and the SACCF shifted southward during the study period (Kim & Orsi, 2014; Sokolov & Rintoul, 2009b) and are projected to shift further southwards as a result of climate change (Graham et al., 2012). While a southward shift of the SAF might have made the SAZ a less favourable region, this study suggests that the long-term poleward shift of the PF and the SACCF might be positive for southern elephant seals in the Atlantic sector. While the shifts in the SAF and the PF were of similar amplitude, the shift of the SACCF was much stronger (Kim & Orsi, 2014). This could explain the long-term trend in the northernmost fronts and zones becoming less favourable areas, whilst particularly being in the SB and the SACCF became more profitable for seals during the study period.

Behavioural strategies in response to environmental heterogeneity

There were quite remarkable inter-annual fluctuations in which frontal systems SOUTHERN ELEPHANT SEALS increased their body condition without any consistent patterns over the years regarding one zone or front becoming a more favourable region than another. This means that overall individuals were able to gain resources irrespective of the exact frontal system they exploited. However, the magnitude of resource gain varied across frontal system. This reflects that some frontal system supported more productivity in some seasons and years than others. However, the very clear pattern of increase in buoyancy, which was consistent irrespective of season and year, suggested that individuals must have been able to compensate for the variability in productivity associated with certain fronts. One possible strategy would be to compensate this spatio-temporal variability by spending time in 3-4 different frontal systems to safeguard being in a profitable region at one point during the migration. Another strategy would be to go to areas in which bottom topography restricts fronts and creates physical boundaries for aggregating prey. In the former case, individuals would search for specific oceanographic conditions that support prey; while in the latter they would respond to changes in prey density brought about by oceanographic features (Dragon et al., 2010). Some evidence for the latter case was provided by the frequent aggregation around shelf areas and bathymetric features such as seamounts. However, most individuals spent time in three or more frontal systems, indicating that changing between fronts and zones was a common strategy. This would indicate that individuals sought specific oceanographic conditions associated with each front or zone that likely supported the desired prey. In fact, the two hypothesouthern elephant seals are not mutually exclusive. It is likely that specific areas within each front or zone were targeted because of bottom topography supported prey aggregations; but that several areas were targeted within different frontal systems to ensure replenishment of resources despite seasonal and inter-annual variations in productivity found in these areas. Indeed, it has been suggested that the inter-individual variability in body condition improvements in and around certain frontal systems and the resultant plasticity with regard to specific systems could indicate differences in foraging behaviour and/or differences in prey preference in specific frontal systems (Abrahms et al., 2018; Field, Bradshaw, Van Den Hoff, Burton, & Hindell, 2007; Field et al., 2004).

In this study, particularly females and/or during the post-breeding migrations, body condition greatly improved north of the PF when AAIW or SW were found at the bottom of dives (Suppl. Figure 12). This suggests that individuals must be feeding very actively and successfully in these waters to sustain these stark improvements in body condition. In more northern frontal systems, the water masses in the upper ocean were particularly important for sustaining these body condition improvements. Previous findings already suggested that while individuals from South Georgia showed body condition improvements in association with these upper layers - particularly AAIW, but also UCDW- individuals from other populations avoided these water masses (Biuw et al., 2007). The improvement in body condition associated with SW north of the PF also correlates with the finding of Hindell et al. (2016) that females increase area-restricted search when in this water mass. However, Hindell et al. (2016) also found males to increase area-restricted search in both UCDW and mCDW. The present analysis revealed almost no body condition improvements when in these two water masses at the bottom of their dives (Suppl. Figure 12). In fact, males in the SACCF even had negative drift rate changes when in UCDW. Although the work by Hindell et al. (2016) included the seals presented here, their analyses were based solely on the horizontal movement patterns (i.e. area restricted search), while we use daily drift rate change as a proxy for successful foraging. This indicates that, although increased area-restricted search is regarded as an indicator of increased foraging activity, increased area-restricted search does not imply successful resource acquisition.

Individuals from Kerguelen have displayed distinct switches in prey in association with either being north or south of the SAF (Vacquié-Garcia et al., 2015). Body condition improvements for males were mostly associated with SW. The prey encounter rate is higher in colder surface waters (Labrousse et al., 2015; Vacquié-Garcia et al., 2015). This suggests that at least males employ a surface foraging strategy when in more southern frontal systems, likely targeting prey such as Antarctic silverfish. For females south of the SAF it does not seem to matter which water mass lies at the bottom of their dives in terms of finding conditions to improve their body condition. This is supported by the fact that there does not seem to be any spatial patterns in prey encounter events related to particular water masses south of the SAF (Vacquié-Garcia et al., 2015). Females thus likely use both a surface and a deep foraging strategy. The association of body condition improvements with mCDW in more southern zones could however also be the result of the high primary and secondary productivity supported by the upwelling of nutrient rich water (Hindell et al., 2016; Labrousse et al., 2015).

Similar patterns were observed for individuals that primarily stayed within four distinct frontal zones, i.e. ‘locals’, and individuals who targeted several frontal systems, i.e. ‘roamers’. ‘Roamers’ primarily improved their body condition in more northern frontal systems and within those in association with upper ocean water masses. ‘Locals’ on the other hand were more frequently in more southern frontal systems, the SB in particular, and body condition improvements were mostly associated with LCDW and its derivatives. However, in the SB ‘locals’ also showed body condition improvements in relation to SW. This suggests that ‘locals’ most likely used both surface and deep foraging strategies, whereas ‘roamers’ primarily focus on surface foraging. Combining these results with the evidence of which sex uses the surface only or the combined surface and deep foraging strategy, it appears likely that most 'locals' are male and 'roamers' are female. Indeed, 22% of the 'locals' were male, while 94% of the 'roamers' were female. Yet, there was insufficient support for this hypothesis due to the underrepresentation of males in this analysis (n_{males}=6 and n_{total} = 49).

Overall, it does appear that the plasticity observed regarding body condition and frontal systems is also displayed in the use and profitability of water masses within these systems. This plasticity revealed here, but also suggested elsewhere (Biuw et al., 2007; Hindell et al., 2016; Labrousse et al., 2015; McIntyre et al., 2015; Muelbert et al., 2013; Vacquié-Garcia et al., 2015), indicates that individuals adjust their behaviour according to the oceanographic environments they encounter. Individuals likely use different foraging strategies to replenish their resources. The choice of water mass is likely primarily determined by the occurrence and profitability of a water mass within a given frontal system (Vacquié-Garcia et al., 2015). The limited amount of evidence for tracing particular water masses across different frontal systems suggests that indeed no particular water masses are targeted, but rather boundary areas at which mixing and aggregation of prey is high.

Conclusion

Despite the variability in which frontal system and water masseswere favourable, southern elephant seals managed to successfully replenish their resources. This indicated that none of the individuals were forced to switch between frontal systems due to the lack of prey, and that individuals could choose between different frontal systems and foraging strategies. The multi-dimensional approach used in this study related changes in the body condition of southern elephant seals to oceanographic features and provided a rough overview of the inter-annual ecosystem productivity. This helped to gain an understanding of the interdependence of biotic and abiotic conditions in this environment. Some changes in the abiotic environment such as positional shifts in fronts and variability associated with frontal position could explain some of the seasonal and inter-annual body condition changes observed in this study. The Southern Ocean and its frontal systems are changing constantly on a range of spatial and temporal scales and we are still developing a better understanding of the physical processes involved in this region (Rintoul, 2018). Therefore, our investigations into the reliance on certain frontal systems and other oceanographic features leaves many open questions as to what the discovered plasticity means for their lifestyle and what this tells about the impacts of the dynamic physical environment, as well as, primary and secondary productivity. Eddies generally increase mixing in the ocean along isopycnals and are thought of being the main driver of mixing across the Antarctic Circumpolar Current. However, more recently it was discovered that their impact is suppressed in the vicinity of the strong frontal jets within the ACC (Naveira-Garabato et al., 2011). This highlights the importance of fronts as favourable foraging regions, even in the vicinity of highly productive cold-water eddies.

The water mass properties in the Southern Ocean have changed over time, with a slight warming of the upper ocean north of the PF and a slight cooling or no change south of the PF (Rhein et al., 2013; Roemmich, Church, Monselesan, Sutton & Wjffels, 2015). This temperature change affects both primary and secondary productivity. However, the present analysis showed that the impact of a temperature change within a frontal system might be small compared to the impact of a reduction in spatial heterogeneity. Climate models predict pronounced changes in the Southern Ocean with stark regional differences (Kirtman et al., 2013). Generally, these predict stronger winds resulting in more eddy kinetic energy especially in the northern part of the ACC, and changing water mass properties at intermediate depths (Meredith, Garabato, Hogg & Farneti, 2012). This could be beneficial for southern elephant seals. However, more in-depth studies focusing on the link between oceanographic features, primary and secondary productivity and top predators are required for gaining a full understanding of the inter-dependence and reliance on certain environmental conditions. Nevertheless, we showed general evidence of resilience against the apparent variability in the location and productivity of frontal systems. This indicates that southern elephant seals appear capable of working with or using the existing variability to their own success. This finding provides a promising outlook for the resilience of the South Georgian southern elephant seal population with regard to climate related changes in the oceanographic environment they inhabit. However, the identification of consistently favourable foraging regions on the basis of frontal systems remains extremely difficult because the resource benefits depend on the individual, sex and season. It is therefore important to integrate more fine-scale behavioural and oceanographic information when using southern elephant seals as sentinels in the future.

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vii. References

Abrahms, B., Scales, K.L., Hazen, E.L., Gograd, S.J., Schick, R.S., Robinson, P.W., & Costa, D.P. (2018). Mesoscale activity facilitates gain in a top predator. *Proceedings of the Royal Society B: Biological Sciences, 285 (1855),* 20181101.

Arhan, M., Naveira Garabato, A. C., Heywood, K. J., & Stevens, D. P. (2002). The Antarctic Circumpolar Current between the Falkland Islands and South Georgia. *Journal of Physical Oceanography*, *32*(6), 1914–1931. http://doi.org/10.1175/1520-0485(2002)032<1914:TACCBT>2.0.CO;2

Aviso. (2016). *SSALTO/DUACS User Handbook: MSLA and (M)ADT Near-Real Time and Delayed Time Products* (5th ed.). CLS-Cnes. Retrieved from http://www.aviso.altimetry.fr/fileadmin/documents/data/tools/hdbk_duacs.pdf

Bailleul, F., Authier, M., Ducatez, S., Roquet, F., Charrassin, J. B., Cherel, Y., & Guinet, C. (2010). Looking at the unseen: Combining animal bio-logging and stable isotopes to reveal a shift in the ecological niche of a deep diving predator. *Ecography*, *33*, 709–719. http://doi.org/10.1111/j.1600-0587.2009.06034.x

Bailleul, F., Charrassin, J.-B., Ezraty, R., Girard-Ardhuin, F., McMahon, C. R., Field, I. C., & Guinet, C. (2007). Southern elephant seals from Kerguelen Islands confronted by Antarctic Sea ice. Changes in movements and in diving behaviour. *Deep Sea Research Part II: Topical Studies in Oceanography*, *54*, 343–355. http://doi.org/http://dx.doi.org/10.1016/j.dsr2.2006.11.005

Bailleul, F., Charrassin, J.-B., Monestiez, P., Roquet, F., Biuw, M., & Guinet, C. (2007). Successful foraging zones of southern elephant seals from the Kerguelen Islands in relation to oceanographic conditions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1487), 2169–2181. http://doi.org/10.1098/rstb.2007.2109

Bailleul, F., Cotté, C., & Guinet, C. (2010). Mesoscale eddies as foraging area of a deep-diving predator, the southern elephant seal. *Marine Ecology Progress Series*, *408*, 251–264. http://doi.org/10.3354/meps08560 MARINE

Behrenfeld, M. J., O'Malley, R. T., Siegel, D. a, McClain, C. R., Sarmiento, J. L., Feldman, G. C., … Boss, E. S. (2006). Climate-driven trends in contemporary ocean productivity. *Nature*, *444*, 752–755. http://doi.org/10.1038/nature05317

Belkin, I. M., & Gordon, A. L. (1996). Southern Ocean fronts from the Greenwich meridian to Tasmania. *Journal of Geophysical Research*, *101*, 3675. http://doi.org/10.1029/95JC02750

Bestley, S., Jonsen, I. D., Hindell, M., Guinet, C., & Charrassin, J.-B. (2013). Integrative modelling of animal movement: incorporating in situ habitat and behavioural information for a migratory marine predator. *Proceedings of The Royal Society B: Biological Sciences*, *280*(1750), 2012–2262. http://doi.org/10.1098/rspb.2012.2262

Biuw, M., Boehme, L., Guinet, C., Hindell, M., Costa, D., Charrassin, J. B., … Fedak, M. A. (2007). Variations in behavior and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 13705–13710. http://doi.org/10.1073/pnas.0701121104

Biuw, M., McConnell, B., Bradshaw, C. J., Burton, H., & Fedak, M. (2003). Blubber and buoyancy: monitoring the body condition of free-ranging seals using simple dive characteristics. *The Journal of Experimental Biology*, *206*, 3405–3423. http://doi.org/10.1242/jeb.00583

Biuw, M., Nøst, O. A., Stien, A., Zhou, Q., Lydersen, C., & Kovacs, K. M. (2010). Effects of Hydrographic Variability on the Spatial, Seasonal and Diel Diving Patterns of Southern elephant seals in the Eastern

Weddell Sea. *PLoS ONE*, *5*(11), e13816. http://doi.org/10.1371/journal.pone.0013816
Boehme, L., Lovell, P., Biuw, M., Roquet, F., Nicholson, J., Thorpe, S. E., … Fedak, M. (2009). Technical Note: Animal-borne CTD-Satellite Relay Data Loggers for real-time oceanographic data collection. *Ocean Science*, *5*, 685–695. http://doi.org/10.5194/os-5-685-2009
Boehme, L., Meredith, M. P., Thorpe, S. E., Biuw, M., & Fedak, M. (2008). Antarctic circumpolar current frontal system in the South Atlantic: Monitoring using merged Argo and animal-borne sensor data. *Journal of Geophysical Research: Oceans*, *113*, 1–19. http://doi.org/10.1029/2007JC004647
Boehme, L., Thompson, D., Fedak, M., Bowen, D., Hammill, M. O., & Stenson, G. B. (2012). How Many Seals Were There? The Global Shelf Loss during the Last Glacial Maximum and Its Effect on the Size and Distribution of Grey Seal Populations. *PLoS ONE*, *7*, e53000. http://doi.org/10.1371/journal.pone.0053000
Boehme, L., Thorpe, S. E., Biuw, M., Fedak, M., & Meredith, M. P. (2008). Monitoring Drake Passage with elephant seals: Frontal structures and snapshots of transport. *Limnology and Oceanography*, *53*, 2350–2360. http://doi.org/10.4319/lo.2008.53.5_part_2.2350
Bornemann, H., Kreyscher, M., Ramdohr, S., Martin, T., Carlini, A., Sellmann, L., & Plötz, J. (2000). Southern elephant seal movements and Antarctic sea ice. *Antarctic Science*, *12*, 3–15.
Bost, C. A., Cotté, C., Bailleul, F., Cherel, Y., Charrassin, J. B., Guinet, C., … Weimerskirch, H. (2009). The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *Journal of Marine Systems*, *78*, 363–376. http://doi.org/http://dx.doi.org/10.1016/j.jmarsys.2008.11.022
Campagna, C., Piola, A. R., Rosa Marin, M., Lewis, M., & Fernández, T. (2006). Southern elephant seal trajectories, fronts and eddies in the Brazil/Malvinas Confluence. *Deep Sea Research Part I: Oceanographic Research Papers*, *53*, 1907–1924. http://doi.org/http://dx.doi.org/10.1016/j.dsr.2006.08.015
Campagna, C., Short, F. T., Polidoro, B. a., McManus, R., Collette, B. B., Pilcher, N. J., … Carpenter, K. E. (2011). Gulf of Mexico Oil Blowout Increases Risks to Globally Threatened Species. *BioScience*, *61*, 393–397. http://doi.org/10.1525/bio.2011.61.5.8
Charrassin, J.-B., Roquet, F., Park, Y.-H., Bailleul, F., Guinet, C., Meredith, M., … Costa, D. P. (2009). New insights into Southern Ocean physical and biological processes revealed by instrumented elephant seals. (J. Hall, H. D.E., & D. Stammer, Eds.) *Proceedings of OceanObs'09: Sustained Ocean Observations and Information for Society*. Venice, Italy: ESA Publication WPP-306.
Cherel, Y., Ducatez, S., Fontaine, C., Richard, P. & Guinet, C. (2008). Stable isotopes reveal the trophic position and mesopelagic fish diet of female southern elephant seals breeding on the Kerguelen Islands. *Marine Ecology Progress Series*, 370, 239-247. https://doi.org/10.3354/meps07673
Constable, A. J., Melbourne-Thomas, J., Corney, S. P., Arrigo, K. R., Barbraud, C., Barnes, D. K. A., … Ziegler, P. (2014). Climate change and Southern Ocean ecosystems I: How changes in physical habitats directly affect marine biota. *Global Change Biology, 20*, 3004–3025. http://doi.org/10.1111/gcb.12623
Costa, D. P., Breed, G. A., & Robinson, P. W. (2012). New Insights into Pelagic Migrations: Implications for Ecology and Conservation. *Annual Review of Ecology, Evolution, and Systematics*, *43*, 73–96. http://doi.org/10.1146/annurev-ecolsys-102710-145045
Cotté, C., D'Ovidio, F., Dragon, A.-C., Guinet, C., & Lévy, M. (2015). Flexible preference of southern elephant seals for distinct mesoscale features within the Antarctic Circumpolar Current. *Progress in Oceanography*, *131*, 46–58. http://doi.org/10.1016/j.pocean.2014.11.011
Crocker, D. E., Costa, D. P., Le Boeuf, B. J., Webb, P. M., & Houser, D. S. (2006). Impact of El Niño on the foraging behavior of female northern elephant seals. *Marine Ecology Progress Series*, *309*, 1–10.
Crocker, D. E., Le Boeuf, B. J., & Costa, D. P. (1997). Drift diving in female northern elephant seals: implications for food processing. *Canadian Journal of Zoology*, *75*, 27–39. http://doi.org/10.1139/z97-004
Davidson, A. D., Boyer, A. G., Kim, H., Pompa-Mansilla, S., Hamilton, M. J., Costa, D. P., … Brown, J. H. (2012). Drivers and hotspots of extinction risk in marine mammals. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 3395–3400. http://doi.org/10.1073/pnas.1121469109
Della Penna, A., De Monte, S., Kestenare, E., Guinet, C., & d'Ovidio, F. (2015). Quasi-planktonic behavior of foraging top marine predators. *Scientific Reports*, *5*(November), 18063. http://doi.org/10.1038/srep18063
Deppeler, S. L. & Davidson, A. T. (2017), Southern Ocean Phytoplankton in a Changing Climate. *Frontiers in Marine Science, 4,* http://doi.org/10.3389/fmars.2017.00040
Dong, S., Sprintall, J., & Gille, S. T. (2006). Location of the Antarctic Polar Front from AMSR-E Satellite Sea Surface Temperature Measurements. *Journal of Physical Oceanography*, *36*, 2075–2089. http://doi.org/10.1175/JPO2973.1
Dragon, A.-C., Monestiez, P., Bar-Hen, A., & Guinet, C. (2010). Linking foraging behaviour to physical oceanographic structures: Southern elephant seals and mesoscale eddies east of Kerguelen Islands. *Progress in Oceanography*, *87*(1–4), 61–71. http://doi.org/10.1016/j.pocean.2010.09.025
Fauchald, P., & Tveraa, T. (2006). Hierarchical patch dynamics and animal movement pattern. *Oecologia*, *149*,

383–395. http://doi.org/10.1007/s00442-006-0463-7

Fedak, M. A., Lovell, P., & Grant, S. M. (2001). Two approaches to compressing and interpreting time-depth information as collected by time-depth recorders and satellite-linked data recorders. *Marine Mammal Science*, *17*, 94–110. http://doi.org/10.1111/j.1748-7692.2001.tb00982.x

Fedak, M., Lovell, P., McConnell, B., & Hunter, C. (2002). Overcoming the Constraints of Long Range Radio Telemetry from Animals: Getting More Useful Data from Smaller Packages. *Integrative and Comparative Biology*, *42*, 3–10. http://doi.org/10.1093/icb/42.1.3

Field, I., Bradshaw, C. A., Burton, H., & Hindell, M. (2004). Seasonal use of oceanographic and fisheries management zones by juvenile southern elephant seals (*Mirounga leonina*) from Macquarie Island. *Polar Biology*, *27*, 432–440. http://doi.org/10.1007/s00300-004-0615-3

Field, I. C., Bradshaw, C. J. A., Van Den Hoff, J., Burton, H. R., & Hindell, M. A. (2007). Age-related shifts in the diet composition of southern elephant seals expand overall foraging niche. *Marine Biology*, *150*, 1441–1452. http://doi.org/10.1007/s00227-006-0417-y

Field, I., Hindell, M., Slip, D., & Michael, K. (2001). Foraging strategies of southern elephant seals (*Mirounga leonina*) in relation to frontal zones and water masses. *Antarctic Science*, *13*, 371–379.

Freeman, N. M., Lovenduski, N. S., & Gent, P. R. (2016). Temporal variability in the Antarctic Polar Front (2002–2014). *Journal of Geophysical Research: Oceans*, *121*, 3372–3380. http://doi.org/10.1002/2015JC011421.Received

Gordine, S. A. (2017). *Pinniped diving behaviour in geographic and oceanographic space*. University of St Andrews.

Gordine, S. A., Fedak, M., & Boehme, L. (2015). Fishing for drifts: detecting buoyancy changes of a top marine predator using a step-wise filtering method. *Journal of Experimental Biology*, *218*, 3816–3824. http://doi.org/doi: 10.1242/jeb.118109

Graham, R. M., De Boer, A. M., Heywood, K. J., Chapman, M. R., & Stevens, D. P. (2012). Southern Ocean fronts: Controlled by wind or topography? *Journal of Geophysical Research: Oceans*, *117*, 1–14. http://doi.org/10.1029/2012JC007887

Guinet, C., Vacquié-Garcia, J., Picard, B., Bessigneul, G., Lebras, Y., Dragon, A. C., … Bailleul, F. (2014). Southern elephant seal foraging success in relation to temperature and light conditions: insight into prey distribution. *Marine Ecology Progress Series*, *499*, 285–301. http://doi.org/10.3354/meps10660

Hakoyama, H., Le Boeuf, B. J., Naito, Y., & Sakamoto, W. (1994). Diving behavior in relation to ambient water temperature in northern elephant seals. *Canadian Journal of Zoology*, *72*, 643–651. http://doi.org/10.1139/z94-087

Herraiz-Borreguero, L., & Rintoul, S. R. (2011). Subantarctic mode water: Distribution and circulation. *Ocean Dynamics*, *61*, 103–126. http://doi.org/10.1007/s10236-010-0352-9

Heywood, K. J., & King, B. A. (2002). Water massouthern elephant seals and baroclinic transports in the South Atlantic and Southern oceans. *Journal of Marine Research*, *60*, 639–676. http://doi.org/10.1357/002224002762688687

Hindell, M. A., Bradshaw, C. J. A., Sumner, M. D., Michael, K. J., & Burton, H. R. (2003). Dispersal of Female Southern elephant seals and Their Prey Consumption during the Austral Summer: Relevance to Management and Oceanographic Zones. *Journal of Applied Ecology*, *40*, 703–715. http://doi.org/10.2307/3505843

Hindell, M. A., Mcmahon, C. R., Bester, M. N., Boehme, L., Costa, D., Fedak, M. A., … Charrassin, J.-B. (2016). Circumpolar habitat use in the southern elephant seal : implications for foraging success and population trajectories . *Ecosphere*, *7*(January), 1–27. http://doi.org/10.1002/ ecs2.1213

Jonker, F. C., & Bester, M. N. (1998). Seasonal movements and foraging areas of adult southern female elephant seals, *Mirounga leonina*, from Marion Island. *Antarctic Science*, *10*, 21–30.

Kim, Y. S., & Orsi, A. H. (2014). On the Variability of Antarctic Circumpolar Current Fronts Inferred from 1992–2011 Altimetry*. *Journal of Physical Oceanography*, *44*, 3054–3071. http://doi.org/10.1175/JPO-D-13-0217.1

Kirtman, B., Power, S.B., Adedoyin, J.A., Boer, G.J., Bojariu, R., Camilloni, I., … Wang, H.J. (2013). Near-term Climate Change: Projections and Predictability. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex & P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA

Labrousse, S., Vacquié-Garcia, J., Heerah, K., Guinet, C., Sallée, J.-B., Authier, M., … Charrassin, J.-B. (2015). Winter use of sea ice and ocean water mass habitat by southern elephant seals: The length and breadth of the mystery. *Progress in Oceanography*, *137*, 52–68. http://doi.org/10.1016/j.pocean.2015.05.023

Levin, P. S., Fogarty, M. J., Murawski, S. A., & Fluharty, D. (2009). Integrated ecosystem assessments: Developing the scientific basis for ecosystem-based management of the ocean. *PLoS Biology*, *7*,

e1000014. http://doi.org/10.1371/journal.pbio.1000014
Lovenduski, N. S., & Gruber, N. (2005). Impact of the Southern Annular Mode on Southern Ocean circulation and biology. *Geophysical Research Letters*, *32*, 1–4. http://doi.org/10.1029/2005GL022727
Massie, P. P., McIntyre, T., Ryan, P. G., Bester, M. N., Bornemann, H., & Ansorge, I. J. (2015). The role of eddies in the diving behaviour of female southern elephant seals. *Polar Biology*, *39*, 297–307. http://doi.org/10.1007/s00300-015-1782-0
McIntyre, T., Donaldson, A., & Bester, M. N. (2015). Spatial and temporal patterns of changes in condition of southern elephant seals. *Antarctic Science*, *10*, 1–10. http://doi.org/10.1017/S0954102015000553
Meredith, M. P., Garabato, A. C. N., Hogg, A. M. & Farneti, R. (2012) Sensitivity of the overturning circulation in the Southern Ocean to decadal changes in wind forcing. *Journal of Climate, 25*, 9–110, https://doi.org/10.1175/2011JCLI4204.1.
Mertz, F., Rosmorduc, V., Maheu, C. and Faugère, Y. (2016). Product user manual: For Sea Level SLA products.2nd ed. EU Copernicus Marine Service.
Miller, P. I., Scales, K. L., Ingram, S. N., Southall, E. J., & Sims, D. W. (2015). Basking sharks and oceanographic fronts: Quantifying associations in the north-east Atlantic. *Functional Ecology*, *29*(8), 1099–1109. http://doi.org/10.1111/1365-2435.12423
Muelbert, M. M. C., de Souza, R. B., Lewis, M. N., & Hindell, M. A. (2013). Foraging habitats of southern elephant seals, *Mirounga leonina*, from the Northern Antarctic Peninsula. *Deep Sea Research Part II: Topical Studies in Oceanography*, *88–89*, 47–60. http://doi.org/http://dx.doi.org/10.1016/j.dsr2.2012.07.009
Murphy, E. J., Hofmann, E. E., Watkins, J. L., Johnston, N. M., Piñones, A., Ballerini, T., … Fretwell, P. (2013). Comparison of the structure and function of Southern Ocean regional ecosystems: The Antarctic Peninsula and South Georgia. *Journal of Marine Systems*, *109–110*, 22–42. http://doi.org/10.1016/j.jmarsys.2012.03.011
Murphy, E. J., Trathan, P. N., Watkins, J. L., Reid, K., Meredith, M. P., Forcada, J., … Rothery, P. (2007). Climatically driven fluctuations in Southern Ocean ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1629), 3057–3067. http://doi.org/10.1098/rspb.2007.1180
Naveria-Garabato, A.C, Ferrari, R. & Polzin, K.L. (2011) Eddy stirring in the Southern Ocean, *JGR:Oceans*, 116, C9. doi:10.1029/2010JC006818
Nicol, S., Pauly, T., Bindoff, N. L., Wright, S., Thiele, D., Hosie, G. W., … Woehler, E. (2000). Ocean circulation off east Antarctica affects ecosystem structure and sea-ice extent. *Nature*, *406*, 504–507. http://doi.org/10.1038/35020053
Orsi, A. H., Whitworth, T., & Nowlin, W. D. (1995). On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Research Part I*, *42*, 641–673. http://doi.org/10.1016/0967-0637(95)00021-W
Photopoulou, T. (2012). *Diving and depth use in seals: inferences from telemetry data using regression and random walk movement models* (Doctor of). *University of St Andrews*. University of St Andrews, St Andrews, Scotland.
Pollard, R. T., Lucas, M. I., & Read, J. F. (2002). Physical controls on biogeochemical zonation in the Southern Ocean. *Deep-Sea Research Part II: Topical Studies in Oceanography*, *49*, 3289–3305. http://doi.org/10.1016/S0967-0645(02)00084-X
R Core Team. (2013). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.r-project.org/
Rhein, M., Rintoul, S. R., Aoki, S., Campos, E., Chambers, D., Feely, R.A., … Wang, F. (2013). *Observations: Ocean.* In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA)
Rintoul, S.R. (2018) The global influence of localized dynamics in the Southern Ocean, *Nature*, 558, 209–218.
Rintoul, S., Hughes, C., & Olbers, D. (2001). The Antarctic Circumpolar Current System. In G. Siedler, J. Church, & J. Gould (Eds.), *Ocean Circulation and Climate* (pp. 271–301). New York: Academic Press. http://doi.org/10.1002/ajp.20122
Robinson, P. W., Simmons, S. E., Crocker, D. E., & Costa, D. P. (2010). Measurements of foraging success in a highly pelagic marine predator, the northern elephant seal. *Journal of Animal Ecology*, *79*, 1146–1156. http://doi.org/10.1111/j.1365-2656.2010.01735.x
Roemmich, D., Church, J., Gilson, J., Monselesan, D., Sutton, P. & Wijffels, S. (2015) Unabated planetary warming and its ocean structure since 2006. *Nature Climate Change*, 5, 240–245.
Roquet, F., Wunsch, C., Forget, G., Heimbach, P., Guinet, C., Reverdin, G., … Fedak, M. A. (2013). Estimates of the Southern Ocean General Circulation Improved by Animal-Borne Instruments. *Geophysical Research Letters*, 2013GL058304. http://doi.org/10.1002/2013GL058304

Saunders, R.A., Collins, M.A., Stowasser, G., & Tarling, G.A. (2017). Southern Ocean mesopelagic fish communities in the Scotia Sea are sustained by mass immigration. *Marine Ecology Progress Series,* 569,173-185. https://doi.org/10.3354/meps12093

Scales, K. L., Miller, P. I., Hawkes, L. A., Ingram, S. N., Sims, D. W., & Votier, S. C. (2014). On the front line: Frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *Journal of Applied Ecology*, *51*, 1575–1583. http://doi.org/10.1111/1365-2664.12330

Schlitzer, R. (2015). Ocean Data Viewer. odv.awi.de. Retrieved from odw.awi.de

Schofield, O., Ducklow, H. W., Martinson, D. G., Meredith, M. P., Moline, M. A., & Fraser, W. R. (2010). How Do Polar Marine Ecosystems Respond to Rapid Climate Change? *Science*, *328*(5985), 1520–1523. http://doi.org/10.1126/science.1185779

Shao, A. E., Gille, S. T., Mecking, S., & Thompson, L. (2015). Properties of the Subantarctic Front and Polar Front from the skewness of sea level anomaly. *Journal of Geophysical Research C: Oceans*, *120*, 5179–5193. http://doi.org/10.1002/2015JC010723

Silk, J.R.D., Thorpe, S.E., Fielding, S., Murphy, E.J., Tratham, P.N., Watkins, J.L., & Hill, S.L. (2016). Environmental correlates of Antarctic krill distribution in the Scotia Sea and southern Drake Passage. *ICES Journal of Marine Science, 73,* 2288-2301.

Simmons, S. E., Crocker, D. E., Kudela, R. M., & Costa, D. P. (2007). Linking foraging behaviour of the northern elephant seal with oceanography and bathymetry at mesoscales. *Marine Ecology Progress Series*, *346*, 265–275. http://doi.org/10.3354/meps07014

Spall, M. A. (1995) Frontogenesis, subduction, and cross-front exchange at upper-ocean fronts. *Journal of Geophysical Research*, 100, 2543–2557.

Sokolov, S., & Rintoul, S. R. (2009a). Circumpolar structure and distribution of the Antarctic circumpolar current fronts: 1. Mean circumpolar paths. *Journal of Geophysical Research: Oceans*, *114*, 1–19. http://doi.org/10.1029/2008JC005108

Sokolov, S., & Rintoul, S. R. (2009b). Circumpolar structure and distribution of the Antarctic circumpolar current fronts: 2. Variability and relationship to sea surface height. *Journal of Geophysical Research: Oceans*, *114*, 1–15. http://doi.org/10.1029/2008JC005248

Talley, L. D., Pickard, G. L., Emery, W. J., & Swift, J. H. (2011). Southern Ocean. In *Descriptive Physical Oceanography* (6th ed., pp. 437–471). London: Elsevier Ltd. Retrieved from http://booksite.elsevier.com/DPO/chapter13.html

Tomczak, M., & Godfrey, J. S. (1994). Regional Oceanography: An Introduction. In *Regional Oceanography* (1st ed., pp. 1–422). Oxford: Elsevier. http://doi.org/10.1016/B978-0-08-041021-0.50003-5

Tosh, C. A., de Bruyn, P. J. N., Steyn, J., Bornemann, H., van den Hoff, J., Stewart, B. S., … Bester, M. N. (2015). The importance of seasonal sea surface height anomalies for foraging juvenile southern elephant seals. *Marine Biology*, *162*, 2131–2140. http://doi.org/10.1007/s00227-015-2743-4

Trathan, P. N., Forcada, J., & Murphy, E. J. (2007). Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability Environmental forcing and Southern Ocean marine predator populations : effects of climate change and variability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, (May), 2351–2365. http://doi.org/10.1098/rstb.2006.1953

Vacquié-Garcia, J., Guinet, C., Laurent, C., & Bailleul, F. (2015). Delineation of the southern elephant seal's main foraging environments defined by temperature and light conditions. *Deep Sea Research Part II: Topical Studies in Oceanography*, *113*, 145–153. http://doi.org/10.1016/j.dsr2.2014.10.029

Van Den Hoff, J., Burton, H. R., Hindell, M. A., Sumner, M. D., & McMahon, C. R. (2002). Migrations and foraging of juvenile southern elephant seats from Macquarie Island within CCAMLR managed areas. *Antarctic Science*, *14*, 134–145. http://doi.org/10.1017/S095410200200069X

Venables, H., Meredith, M. P., Atkinson, A., & Ward, P. (2012). Fronts and habitat zones in the Scotia Sea. *Deep-Sea Research Part II: Topical Studies in Oceanography*, *59–60*, 14–24. http://doi.org/10.1016/j.dsr2.2011.08.012

Williams, G. D., Hindell, M., Houssais, M. N., Tamura, T., & Field, I. C. (2011). Upper ocean stratification and sea ice growth rates during the summer-fall transition, as revealed by Elephant seal foraging in the Adélie Depression, East Antarctica. *Ocean Science*, *7*, 185–202. http://doi.org/10.5194/os-7-185-2011

viii. Tables

Front/Zone		*p* (in dbar)	Potential temperature (in °C)
STZ		100	$\theta > 12.01$
STF		100	$10.00 < \theta < 12.01$
SAZ		100	$\theta \leq 10.00$
		300	$\theta \geq 4.01$
SAF		300	$4.00 < \theta < 4.01$
PFZ		200	$\theta \geq 2.01$
		300	$\theta \leq 4.00$
PF		200	$2.00 < \theta < 2.01$
	or	[100,300]	$2.00 < \theta min < 2.01$
AAZ		200	$\theta \leq 2.00$
		500	$\theta \geq 1.81$
	or	[100,300]	$\theta min \leq 2.00$
		500	$\theta \geq 1.81$
SACCF		500	$1.80 < \theta < 1.81$
SB		500	$\theta \leq 1.80$
SAZ to PF		100	$\theta \leq 10.00$
	or	[100,300]	$\theta min \geq 2.01$
South of PF		200	$\theta \leq 2.00$
	or	[100,300]	$\theta min \leq 2.00$

Table 1 *Potential temperature ranges for defining oceanographic fronts and zones in the Atlantic sector. P refers to pressure, which describes the depth or depth range. Ranges are indicated by square brackets. If a CTD profile's temperature measurements at a given depth or within a given depth range were of the described potential temperature, then this CTD profile was assigned to the respective front or zone.*

	pot.temp	Adt	merged
STZ	44	265	47
STF	286	346	370
SAZ	2038	1289	2131
SAF	6	622	65
PFZ	4267	3025	4500
PF	49	1657	115
AAZ	4005	4869	6689
SACCF	55	2290	1205
SB	6008	7692	9128
SAZ to PFZ	326		101
South of PF	8627		2415
undefined	1927	5583	872
total	27638	27638	27638

Table 2 *Amount of unique CTD profiles recorded in each frontal system. The frontal systems were determined using different approaches. 'Pot.temp' refers to the potential temperature approach. 'Adt', and 'merged' correspond to approaches based on dynamic height or a combination of potential temperature and dynamic height. These approaches will be explained in the following sections.*

Frontal range	Water mass	Neural density (γ^n)	Potential temperature (Θ) in °C	Water depth (d_w) in m
North of SAF (SAZ, STF, STZ)	SW	$\gamma^n \leq 27.15$		
	SAMW	$27.15 < \gamma^n \leq 27.35$		
	AAIW	$27.35 < \gamma^n \leq 27.55$		
	UCDW	$27.55 < \gamma^n \leq 27.92$		
	NADW	$27.92 < \gamma^n \leq 28.11$		
	LCDW	$28.11 < \gamma^n \leq 28.26$		
	AABW	$28.26 < \gamma^n$		
SAF to SB (PF, PFZ, SAF, SACCF, AAZ)	AAIW [SAF, PFZ, PF] SW [AAZ, SACCF]	$\gamma^n \leq 27.55$		
	UCDW	$27.55 < \gamma^n \leq 28.00$		
	LCDW1	$28.00 < \gamma^n \leq 28.09$		
	LCDW2	$28.09 < \gamma^n \leq 28.26$		
	WSDW [-70°, 30°] LON AABW [-120°, -70°] LON	$28.26 < \gamma^n$		
Within SB (SB)	SW	$\gamma^n \leq 28.00$	$\Theta > -1.95$	
	LCDW	$28.00 < \gamma^n \leq 28.26$	$\Theta > 1.50$	
	mCDW	$28.00 < \gamma^n \leq 28.26$	$\Theta \leq 1.50$	
	WSDW [-70°, 30°] LON	$28.26 < \gamma^n \leq 28.40$	$-0.70 < \Theta < 0.00$	
	mSW	$\gamma^n > 28.27$		$d_w < 2500$
	WSBW [-70°, 30°] LON	$28.40 < \gamma^n$	$\Theta < -0.70$	
	AABW [-120°, -70°] LON	$28.26 < \gamma^n$		
	ISW		$\Theta \leq -1.95$	
For generic grouping 'South of PF'	SW	$\gamma^n \leq 27.55$	$\Theta > -1.95$	
	LCDW	$28.00 < \gamma^n \leq 28.26$	$\Theta > 1.50$	
	mCDW	$28.00 < \gamma^n \leq 28.26$	$\Theta \leq 1.50$	
	AABW [-120°, -70°] LON	$28.26 < \gamma^n$		
	WSDW [-70°, 30°] LON	$28.26 < \gamma^n \leq 28.40$	$-0.70 < \Theta < 0.00$	
	WSDW [-70°, 30°] LON	$\gamma^n > 26.26$	$\Theta > 0.00$	
	WSBW [-70°, 30°] LON	$28.40 < \gamma^n$	$\Theta < -0.70$	
	mSW	$28.27 < \gamma^n$		$d_w < 2500$
	ISW		$\Theta \leq -1.95$	
For generic grouping 'SAZ to PFZ'	UCDW	$27.55 < \gamma^n \leq 28.00$		
	LCDW1	$28.00 < \gamma^n \leq 28.09$		
	LCDW2	$28.09 < \gamma^n \leq 28.26$		
	WSDW [-70°, 30°] LON AABW [-120°, -70°] LON	$28.26 < \gamma^n$		

Table 4 *Definition of water masses in the Atlantic sector within each frontal system. The acronyms refer to: AABW- Antarctic Bottom Water; AAIW – Antarctic Intermediate Water; ISW – Ice Shelf Water; LCDW – Lower Circumpolar Deep Water; LCDW1 – low salinity Lower Circumpolar Deep Water; LCDW2 – high salinity Lower Circumpolar Deep Water; mCDW – modified Circumpolar Deep Water; mSW – modified Surface Water; NADW – North Atlantic Deep Water; SAMW – Subantarctic Mode Water; SW – Surface Water; UCDW – Upper Circumpolar Deep Water; WSBW – Weddell Sea Bottom Water; WSDB – Weddell Sea Deep Water.*

		2005 S	2005 W	2008 S	2008 W	2009 S	2009 W	2010 S	2010 W
STZ	Min			-0.113	0.405	0.123	0.189		
	1st			0.125	0.437	0.123	0.213		
	2nd			0.230	0.437	0.200	0.251		
	3rd			0.387	0.437	0.200	0.356		
	Max			0.568	0.437	0.273	0.359		
	Final	>0.249	>0.296	0.307; 0.568	0.405; 0.437	0.200; 0.273	0.213; 0.359		
STF	Min	0.192	0.199	-0.136	0.060	-0.232	0.049		
	1st	0.210	0.262	0.065	0.195	0.178	0.157		
	2nd	0.215	0.276	0.164	0.240	0.211	0.266		
	3rd	0.249	0.296	0.307	0.265	0.232	0.315		
	Max	0.280	0.336	0.655	0.435	0.263	0.350		
	Final	0.210; 0.249	0.266; 0.296	0.233; 0.307	0.213; 0.265	0.178; 0.200	0.157; 0.213	>0.386	>0.385
SAZ	Min	-0.109	-0.285	-0.332	-0.153	-0.443	-0.471	-0.094	-0.333
	1st	-0.013	0.167	0.004	0.067	-0.084	-0.105	0.220	0.159
	2nd	0.074	0.225	0.135	0.138	0.042	-0.032	0.237	0.225
	3rd	0.190	0.266	0.233	0.213	0.128	0.044	0.263	0.260
	Max	0.254	0.364	0.526	0.285	0.287	0.208	0.386	0.385
	Final	-0.013; 0.190	0.167; 0.266	0.004; 0.233	0.067; 0.213	-0.084; 0.128	-0.105; 0.044	0.220; 0.263	0.159; 0.260
SAF	Min			-0.232	-0.156		0.032		0.222
	1st			-0.232	-0.156		0.032		0.222
	2nd			-0.120	-0.156		0.032		0.222
	3rd			-0.120	-0.156		0.032		0.222
	Max			-0.120	-0.156		0.032		0.222
	Final	-0.359; -0.109	-0.422; -0.285	-0.232; -0.120	-0.108; -0.156	-0.451; -0.443	-0.300; -0.105	-0.539; -0.094	-0.333; -0.396
PFZ	Min	-1.010	-1.048	-1.161	-1.123	-1.260	-1.122	-1.080	-0.595
	1st	-0.586	-0.626	-0.593	-0.624	-0.576	-0.509	-0.645	-0.499
	2nd	-0.522	-0.576	-0.375	-0.578	-0.516	-0.432	-0.587	-0.464
	3rd	-0.359	-0.422	-0.213	-0.542	-0.451	-0.300	-0.539	-0.396
	Max	0.256	0.248	-0.307	-0.108	0.192	0.045	0.290	0.316
	Final	-0.567; -0.359	-0.626; -0.422	-0.593; -0.232	-0.624; -0.542	-0.576; -0.451	-0.509; -0.300	-0.645; -0.539	-0.499; -0.396
PF	Min	-0.948	-1.123	-0.855		-1.170	-0.686	-0.931	
	1st	-0.572	-0.681	-0,855		-1.081	-0.686	-0.820	
	2nd	-0.567	-0.656	-0.745		-0.685	-0.686	-0.734	
	3rd	-0.510	-0.574	-0.623		-0.556	-0.686	-0.642	
	Max	-0.510	-0.574	-0.623		-0.462	-0.686	-0.544	
	Final	-0.572; -0.567	-0.681; -0.626	-0.836; -0.623	-0.745; -0.624	-0.685; -0.576	-0.542; -0.509	-0.722; -0.645	-0.575; -0.499
AAZ	Min	-1.218	-1.136	-1.210	-1.161	-1.211	-1.185	-1.142	-0.640
	1st	-0.961	-1.034	-0.958	-0.966	-0.965	-0.996	-0.934	-0.626
	2nd	-0.882	-0.978	-0.933	-0.943	-0.878	-0.879	-0.871	-0.601
	3rd	-0.850	-0.914	-0.836	-0.927	-0.671	-0.799	-0.722	-0.582
	Max	-0.523	-0.422	-0.236	-0.546	-0.381	-0.542	-0.427	-0.575
	Final	-0.961; -0.850	-1.005; -0.914	-0.982; -0.836	-0.966; -0.927	-0.985; -0.685	-0.996; -0.799	-0.934; -0.722	-0.626; -0.582
SACCF	Min	-1.127	-1.041	-1.068	-1.143	-1.233	-1.152	-1.077	
	1st	-1.127	-1.034	-1.035	-1.139	-1.137	-1.088	-1.068	
	2nd	-1.104	-1.020	-1.000	-1.122	-1.120	-1.065	-0.979	
	3rd	-1.008	-1.005	-0.985	-1.109	-1.000	-1.052	-0.933	

	Max	-1.080	-0.999	-0.982	-1.076	-0.616	-1.009	-0.930	
	Final	-1.080; -1.104	-1.034; -1.005	-0.982; -1.068	-1.139; -1.109	-1.135; -1.000	-1.088; -1.005	-1.028; -0.934	
SB	Min	-1.277	-1.303	-1.518	-1.548	-1.456	-1.513	-1.201	
	1st	-1.164	-1.257	-1.356	-1.466	-1.294	-1.402	-1.133	
	2nd	-1.114	1.219	-1.250	-1.418	-1.220	-1.313	-1.078	
	3rd	-1.082	-1.095	-1.165	-1.268	-1.135	-1.215	-1.028	
	Max	-0.924	-0.897	-0.281	-0.784	-0.414	-0.975	-0.868	
	Final	-1.228; -1.104	-1.303; -1.095	-1.518; -1.165	-1.548; -1.268	-1.456; -1.135	-1.513; -1.215	-1.201; -1.028	
SAZtoPFZ	Min	-0.918	-0.898	-0.676	0.130	-0.751	-0.501	-0.754	-0.524
	1st	-0.641	0.082	-0.634	0.130	-0.547	-0.452	-0.582	-0.432
	2nd	-0.561	0.198	-0.551	0.130	-0.514	-0.403	-0.521	-0.132
	3rd	-0.330	0.226	0.020	0.130	-0.475	-0.057	-0.493	0.213
	Max	-0.167	0.311	0.516	0.130	-0.254	-0.057	0.413	0.350
southPF	Min	-1.276	-1.302	-1.496	-1.500	-1.446	-1.476	-1.224	-0.642
	1st	-1.115	-1.097	-1.153	-1.221	-1.149	-1.334	-1.094	-0.633
	2nd	-1.014	-1.030	-0.938	-1.111	-1.009	-1.282	-0.945	-0.633
	3rd	-0.872	-0.958	-0.914	-0.918	-0.778	-1.148	-0.757	-0.603
	Max	-0.522	-0.544	-0.391	-0.745	-0.398	-0.605	-0.473	-0.580

Table 3 *Adjusted dynamic height ranges for year and season using 5-number summaries. These ranges were implemented to define fronts and zones on the basis of dynamic height.*

Locals		**Roamers**	
ct8-2849-05	ct40-43589-08	ct8-26626-05	ct49-92571-09
ct8-1553-05	ct45-48919-08	ct8-28494-05	ct49-26629-09
ct8-26631-05	ct49-92575-09	ct8-16624-05	ct49-92573-09
ct8-1549-05	ct49-92576-09	ct8-5811-05	ct49-92568-09
ct40-17219-08	ct49-92570-09	ct8-26623-05	ct49-92569-09
ct40-43876-08	ct49-92567-09	ct40-43876-08	ct49-22496-09
ct40-5813-08	ct58-1554-09	ct40-43881-08	ct49-92574-09
ct40-20915-08	ct58-2840-09	ct45-22498-08	ct58-2242-09
ct40-26632-08	ct65-22496-10	ct45-43849-08	ct58-48930-09
		ct45-43850-08	ct58-2846-09
		ct45-22486-08	ct58-38578-09
		ct45-22489-08	ct58-43863-09
		ct45-22483-08	ct58-48924-09
		ct45-48921-08	ct58-28487-09
		ct45-48922-08	ct58-48926-09
		ct49-92572-09	ct65-22488-10

Table 5 *Categorisation of individual seals as 'locals' and 'roamers'*

Water mass	**frequency**	**%**
SW	257218	59.006
SAMW	0	0.000
AAIW	34719	7.965

UCDW	60187	13.807
ISW	624	0.143
mSW	1512	0.347
LCDW	863	0.198
LCDW1	242	0.0005
LCDW2	4	0.000009
mCDW	38056	8.730
WSBW	1	0.000002
NA	42493	9.745
total	**435919**	**100**

Table 6 *Amounts and percentage of CTD measurements recorded in each water mass.*

ix. Figure legends

Fig. 1 *The amount of time each individual spent in a given front or zone (defined using the merged approach). The two generic groupings are depicted at the bottom. Large individual variation is apparent.*

Fig. 2 *Percentage of time spent in a certain frontal system (determined using the merged approach) varied between the sexes (F = female, M = male) and the seasons (post-moult, post-breeding).*

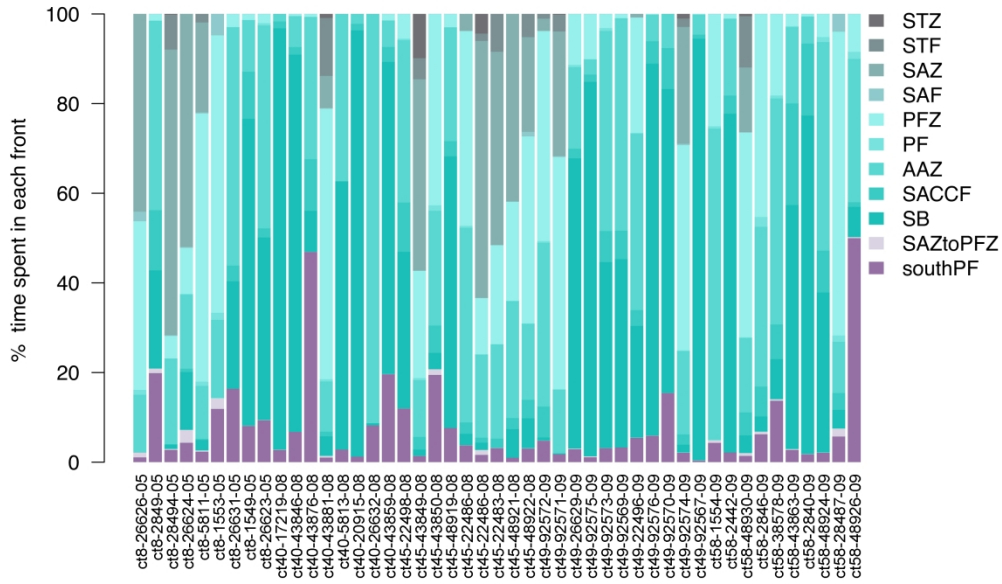
Fig.3 *The boxplots depict the daily drift rate changes whilst individuals were in a given front or zone (defined using the merged approach) during a given migratory period. The fronts and zones depicted on the x-axis, from left to right, were: STZ, STF, SAZ, SAF, PFZ, PF, AAZ, SACCF, SB. Following, northern frontal systems are towards the left, whilst southern frontal systems are more towards the right. Above the green line, individuals generally improved their body condition in a given front/zone, whilst below the line body condition worsened.*

Fig.4 *The Sea Level Anomaly variance for two fronts and their adjacent zones indicate how variable the position of the respective fronts and zones were between November 2009, December 2009, the entire 2009 post-breeding period and the entire period between 2008 and 2010.The arrows indicate the reduction in Sea Level Anomaly variance.*

Fig.5 *The proportion of time females (during the post-moult and post-breeding migrations) and males (during the post-moult migrations) were diving in a given water mass at the bottom of their dives.*

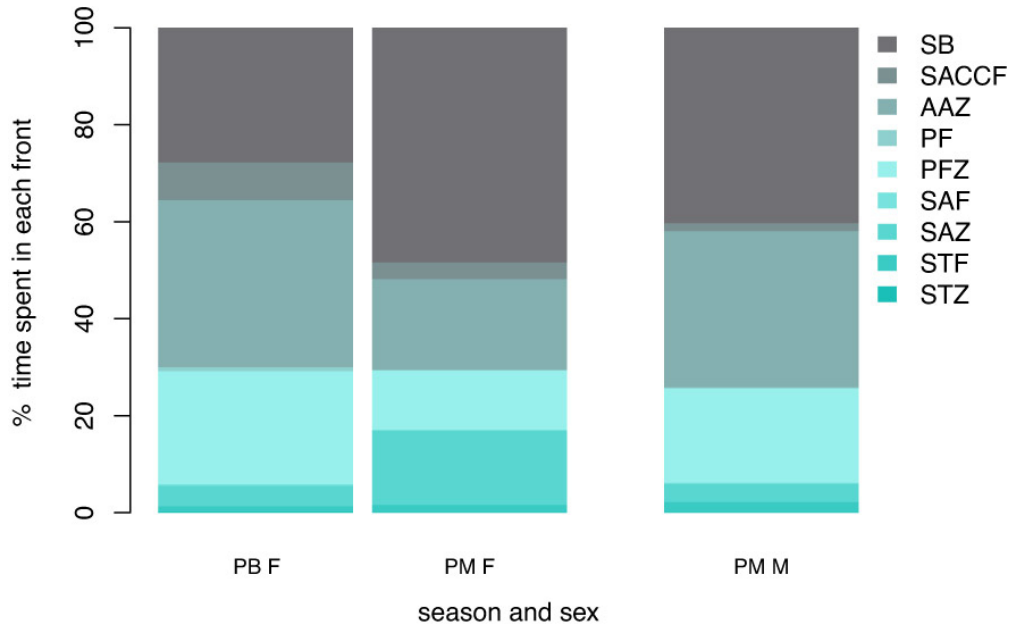
Fig,6 *Heatmap depicting the daily drift rate change 'roamers' (left) and 'locals' (right) were experiencing whilst they were in a given front/zone and in a given water mass at the bottom of their dives.*

Fig.7 *Heatmap depicting the daily drift rate changes individuals were experiencing during the post-moult (left) and post-breeding (right) migrations whilst they were in a given front/zone and in a given water mass at the bottom of their dives. Which water mass in which front supported these positive drift rate changes varied strongly between post-moult (PM) and post-breeding (PL) migrations.*



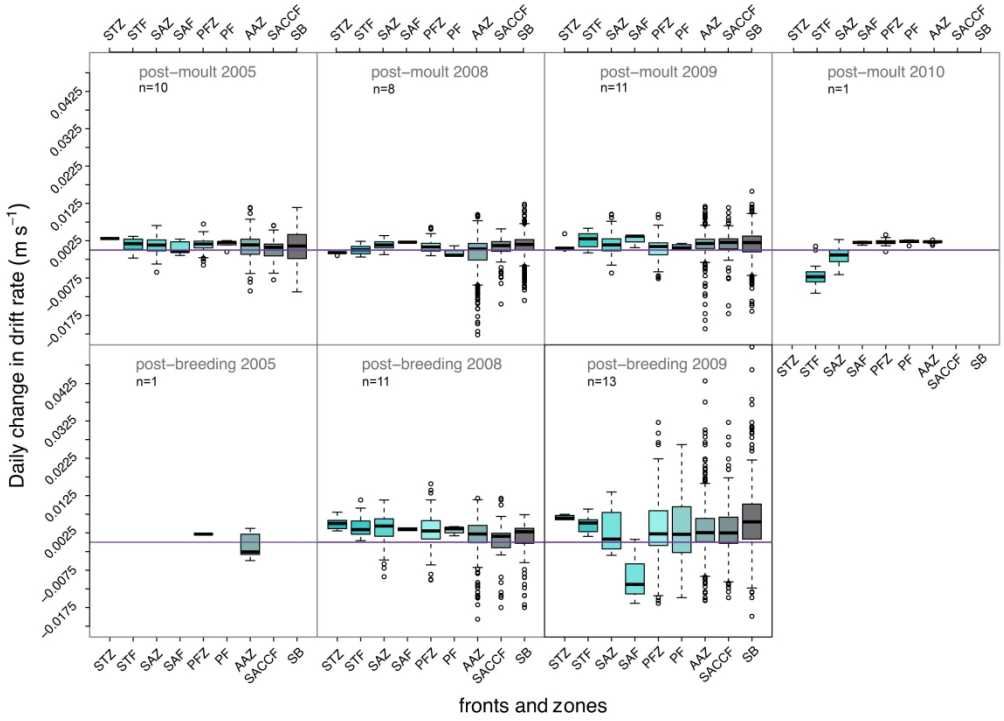
The amount of time each individual spent in a given front or zone (defined using the merged approach). The two generic groupings are depicted at the bottom. Large individual variation is apparent.

239x159mm (300 x 300 DPI)



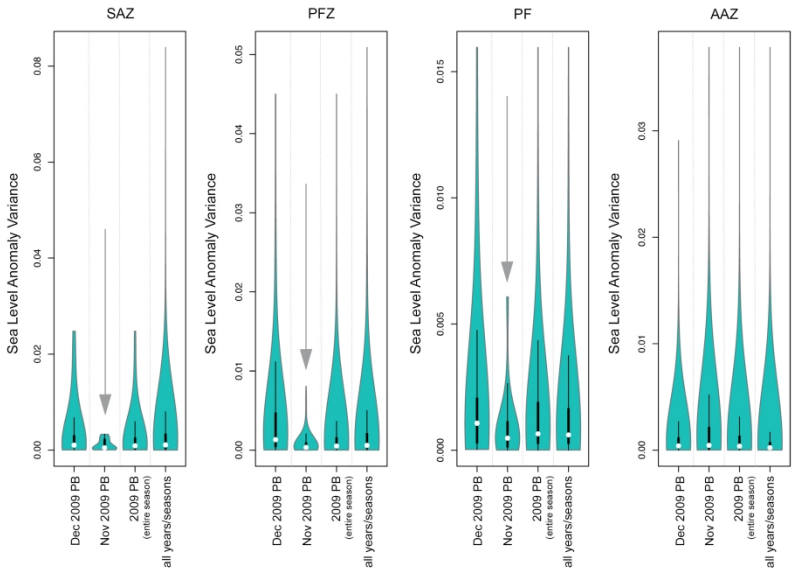
Percentage of time spent in a certain frontal system (determined using the merged approach) varied between the sexes (F = female, M = male) and the seasons (post-moult, post-breeding).

149x93mm (150 x 150 DPI)



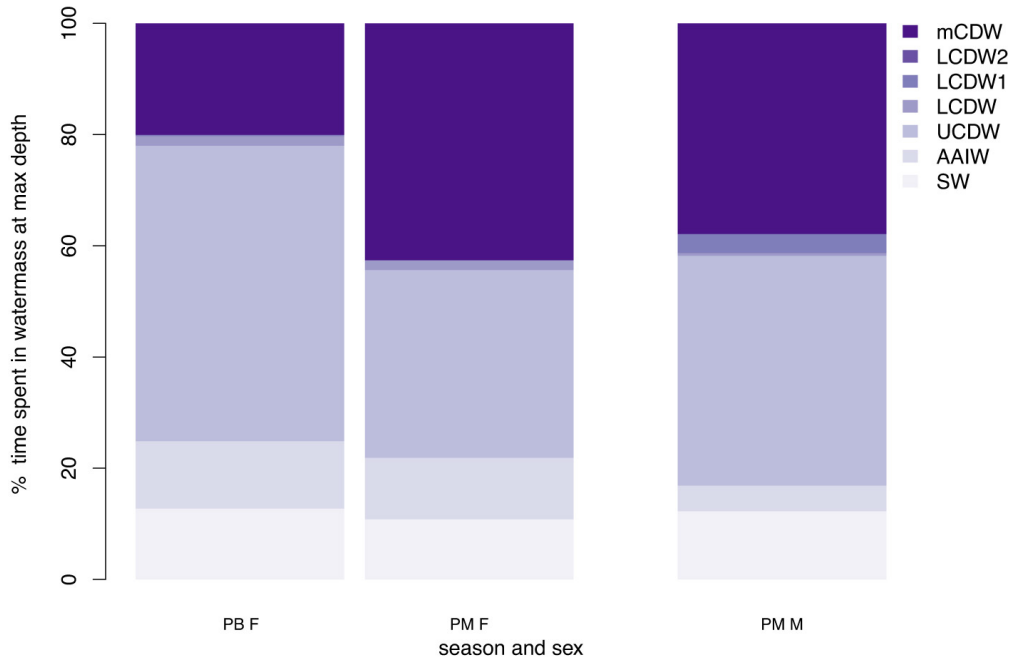
The boxplots depict the daily drift rate changes whilst individuals were in a given front or zone (defined using the merged approach) during a given migratory period. The fronts and zones depicted on the x-axis, from left to right, were: STZ, STF, SAZ, SAF, PFZ, PF, AAZ, SACCF, SB. Following, northern frontal systems are towards the left, whilst southern frontal systems are more towards the right. Above the green line, individuals generally improved their body condition in a given front/zone, whilst below the line body condition worsened.

245x176mm (300 x 300 DPI)



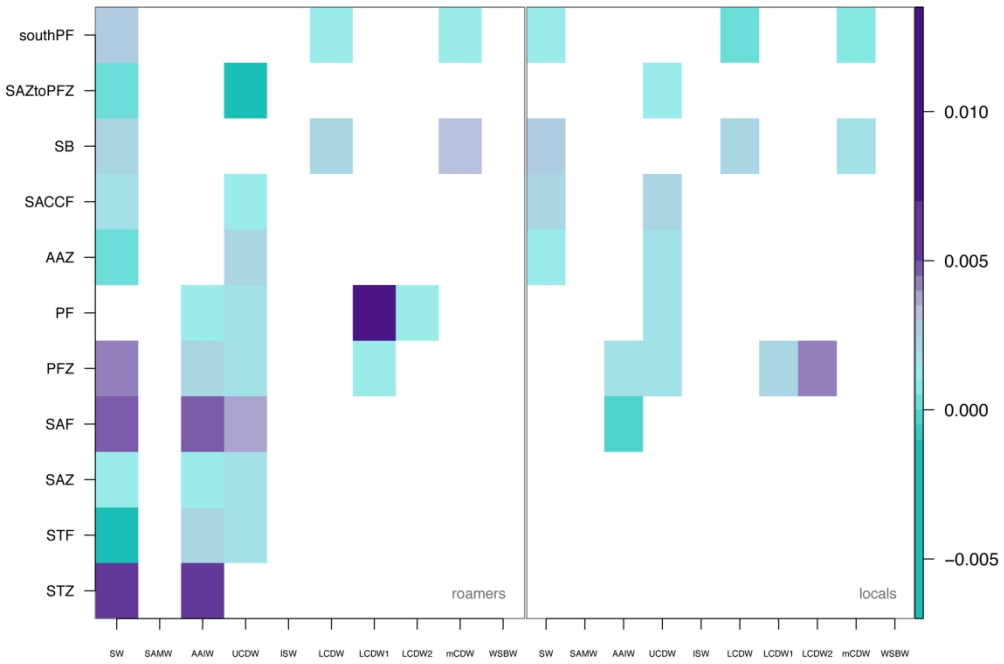
The Sea Level Anomaly variance for two fronts and their adjacent zones indicate how variable the position of the respective fronts and zones were between November 2009, December 2009, the entire 2009 post-breeding period and the entire period between 2008 and 2010.The arrows indicate the reduction in Sea Level Anomaly variance.

297x209mm (300 x 300 DPI)



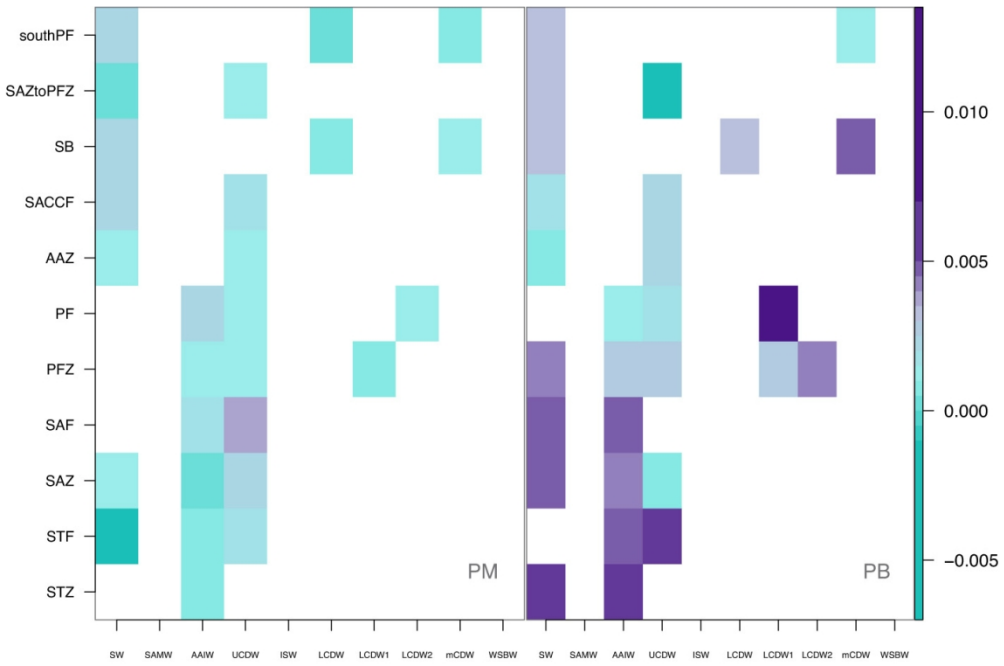
The proportion of time females (during the post-moult and post-breeding migrations) and males (during the post-moult migrations) were diving in a given water mass at the bottom of their dives.

237x156mm (150 x 150 DPI)



Heatmap depicting the daily drift rate change 'roamers' (left) and 'locals' (right) were experiencing whilst they were in a given front/zone and in a given water mass at the bottom of their dives.

239x157mm (300 x 300 DPI)



Heatmap depicting the daily drift rate changes individuals were experiencing during the postmoult (left) and post-breeding (right) migrations whilst they were in a given front/zone and in a given water mass at the bottom of their dives. Which water mass in which front supported these positive drift rate changes varied strongly between post-moult (PM) and post-breeding (PB) migrations.

239x159mm (150 x 150 DPI)